TEXT-BOOK OF PALAEONTOLOGY

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TEXT-BOOK

OF

PALAEONTOLOGY

BY

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PREFACE

SINCE the publication of the first English edition of this volume in 1902, so many discoveries have been made that it is now necessarily enlarged. I have revised the old text, and have re-written much of it while incorporating the new facts; but the form of the book remains the same, and Zittel's method has been followed throughout. In most cases the descriptions of genera are not diagnoses, but merely refer to some striking features. There is sometimes a little conservatism, and groups which are very imperfectly known, such as the higher Teleostean Fishes, modern Amphibians, Lizards, Snakes, and Birds, are still classified only in a general way. The newer literature has been added to the bibliographies, often with abbreviated titles, and many of the older references have been omitted because these are given in the papers quoted.

Most of the old figures of actual fossils, which Zittel preferred to diagrams, have been retained; while changes in nomenclature and any errors that have been detected in the restorations are noted in the descriptive legends. New figures have been added from the fourth German edition (1923), besides many diagrammatic figures from more recent original papers. Two diagrams (Figs. 341, 348) have been specially drawn for this volume by Dr. Robert Broom, F.R.S.

I have to thank especially Dr. Broom, Baron F. Nopcsa, and Baron F. von Huene for help with the fossil Reptiles, Mr. W. P. Pycraft for advice on Birds, and Miss Dorothea M. A. Bate and Dr. K. Lambrecht for many references to fossil Birds.

ARTHUR SMITH WOODWARD

HILL PLACE, HAYWARDS HEATH,
SUSSEX, *April* 1932.

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Phylum VIII. VERTEBRATA[1]

Bilaterally symmetrical animals, with a cartilaginous or ossified vertebral axis, which is usually composed of a series of similar segments, the same supporting the central nervous system above and dividing the trunk into a dorsal and a ventral portion. Never more than two pairs of limbs.

The vertebral column develops from a rod-like cellular tissue of gelatinous consistency (*chorda dorsalis*), of which the outer (skeletogenous) layer gradually subdivides into a number of similar segments, which are originally cartilaginous but subsequently calcified by the deposition of phosphate of lime or are replaced by bone substance. At the anterior end of the vertebral column is the cranial capsule enclosing the brain, also the visceral skeleton. The appendicular skeleton is likewise preformed in cartilage, and among the higher Vertebrata usually develops completely into bone substance. Only some of the lowest Vertebrata exhibit a persistently cartilaginous internal skeleton. The calcification of the cartilage in the sharks and skates takes place in such a way that a homogeneous limy substance is deposited between the cartilage cells, while in ossification the original cartilage cells disappear, and by resorption of the intercellular substance there arise canals with blood-vessels (Haversian canals) as well as small hollow spaces (lacunae, bone corpuscles) filled with bone cells (osteoblasts). The latter are connected with the Haversian canals by very fine tubules (*primitivröhrchen*) radiating in all directions. In many fishes the lacunae (bone corpuscles) are wanting, so that the primitive tubules arise directly from the Haversian canals.

The skeleton of the extremities consists of several articulated segments

[1] *Abel, O.*, Grundzüge der Paläobiologie der Wirbeltiere. Stuttgart, 1912.—Die Stämme der Wirbeltiere. Leipzig, 1919.—*Cope, E. D.*, Syllabus of Lectures on the Vertebrata. Univ. Pennsylvania, Philadelphia, 1898.—*Dollo, L.*, Carpus und Tarsus. Wilhelm Roux' Archiv f. Entwicklungsmech. Organismen, vol. cxx., p. 272, 1929.—*Edinger, T.*, Die fossilen Gehirne. Ergebn. Anat. u. Entwickl. (III. Abt. Zeitschr. gesammt. Anat.), vol. xxviii., p. 1, 1929.—*Gegenbaur, C.*, Vergleichende Anatomie der Wirbeltiere, vols. i., ii. Leipzig, 1898–1901.—*Goodrich, E. S.*, Studies on the Structure and Development of Vertebrates. London, 1930.—*Hay, O. P.*, Bibliography and Catalogue of the Fossil Vertebrata of North America. Bull. U.S. Geol. Surv., no. 179, 1902.—Second Bibliography and Catalogue, vols. i., ii., Carnegie Institution, Publ. no. 390, 1929–30.—*Jaekel, O.*, Die Wirbeltiere. Berlin, 1911.—Kopf der Wirbeltiere. Zeitschr. gesammt. Anatomie, vol. xxvii., pt. iii., p. 815, 1927.—Atemorgane der Wirbeltiere. Zool. Anzeig., vol. lxx., p. 273, 1927; also Palaeont. Zeitschr., vol. ix., p. 250, 1927.—*Kingsley, J. S.*, The Vertebrate Skeleton. Philadelphia and London, 1925.—Comparative Anatomy of Vertebrates, ed. 3. Philadelphia, 1926.—*Lull, R. S.*, Organic Evolution. New York, 1922.—*Owen, R.*, Odontography. London, 1840-45.—*Stromer von Reichenbach, E.*, Lehrbuch der Paläozoologie, II. Wirbeltiere. Leipzig, 1912.—*Woodward, A. S.*, Outlines of Vertebrate Palaeontology. Cambridge, 1898.—*Woodward, A. S.*, and *Sherborn, C. D.*, Catalogue of British Fossil Vertebrata. London, 1890.

which exhibit an extraordinarily varied arrangement according to the function of the limbs.

The nervous system consists of a central organ divided into brain and spinal chord, from which numerous nerves arise and extend throughout the whole of the body. The blood is first driven to the organs of respiration (gills or lungs) by means of a heart provided with one or two auricles, and after it has traversed the body in numerous arteries and veins it returns to the heart. The oesophagus, stomach, intestine, liver, kidneys, and spleen, as well as the organs of generation, lie in the ventral part of the body. The skin is often provided with hairs, spines, scales, feathers, or bony plates.

As a rule only remains of the bony skeleton, teeth, or hard ossified parts of the skin are available to the palaeontologist for investigation; but these can generally be determined with great certainty.

The following five Classes of Vertebrates are distinguished:—*Pisces*, *Amphibia*, *Reptilia*, *Aves*, and *Mammalia*. The groups of *Tunicata* and *Leptocardii* have been placed with these as special Classes and often regarded as the ancestors of the Vertebrates. As these have left no fossil remains in the rocks, the palaeontologist discovers no clue to the origin of the *Vertebrata*.

The four higher Classes of Vertebrates above *Pisces* are grouped sometimes under the name *Tetrapoda* (four-footed), sometimes as *Stapedifera* (bearing a *stapes* or ear bone, which is equivalent to the hyomandibular bone of *Pisces*).

Class 1. PISCES.[1] Fishes.

Cold-blooded animals living in water and usually breathing exclusively by gills. Vertebral axis ending in a vertical caudal fin. Limbs in the form of fins. Skin with scales or bony plates, rarely naked. Heart with a single ventricle and auricle. No amnion or allantois.

To the skin structures of fishes belong the scales, dermal bones, spines, fin rays, and teeth.

[1] *Agassiz, L.*, Recherches sur les poissons fossiles, vols. i.-v. Neuchâtel et Soleure, 1833-44. —Monographie des poissons fossiles du Vieux Grès Rouge. Neuchâtel et Soleure, 1844-45.—*Bridge, T. W.*, Fishes. In Cambridge Natural History, vol. on Fishes, etc., p. 139. London, 1904.—*Broom, R.*, Fossil Fishes of Upper Karroo Beds of South Africa. Ann. S. African Mus., vol. vii., p. 251, 1909.—Fishes from the Lower and Middle Karroo Beds. *Loc. cit.*, vol. xii., p. 1, 1913.—Fossil Fishes in Albany Museum. Rec. Albany Mus., vol. ii., p. 391, 1912.—*Brough, J.*, Fossil Fishes from the Karroo System, and some General Considerations on the Bony Fishes of the Triassic Period. Proc. Zool. Soc., 1931, p. 235.—*Chapman, F.*, Cretaceous and Tertiary Fish-Remains of New Zealand. Geol. Surv. N. Zealand, Palaeont. Bull., no. 7, 1918.—*Chapman, F.*, and *Cudmore, F. A.*, Australian Cainozoic Fish-Remains. Proc. Roy. Soc. Vict., n.s., vol. xxxvi., p. 107, 1924.—*Chapman, F.*, and *Pritchard, G. B.*, Fish Remains from Tertiaries of Australia. Proc. Roy. Soc. Vict., n.s, vols. xvii., p. 267, xx., p. 59, 1904, 1907.—*Cuvier* et *Valenciennes*, Histoire naturelle des poissons, 22 vols. Paris, 1828-49.—*Davis, J. W.*, Fossil Fishes of the Carboniferous Limestone Series of Great Britain. Trans. Roy. Dublin Soc. [2], vol. i., p. 327, 1883.—Fossil Fishes of the Chalk of Mount Lebanon. *Loc. cit.*, vol. iii., p. 457, 1887.—Fossil Fish Remains from Tertiary and Cretaceo-Tertiary of New Zealand. *Loc. cit.*, vol. iv., p. 1, 1888.—Fossil Fish of the Cretaceous Formations of Scandinavia. *Loc. cit.*, vol. iv., p. 363, 1890.—*Dean, B.*, Bibliography of Fishes. 3 vols. Amer. Mus. Nat. Hist., New York, 1916-23.—*de Beaufort, L. F.*, Upper Cretaceous Teeth and other Vertebrate Remains from a Deep Sea Deposit in the Island of Timor. Jaarb. Mijnw. Nederl. O.-Indië Verh., 1920, iv., p. 61, 1923.—Marine Fishes from the Miocene of South Celebes. *Loc. cit.*, 1925, p. 117, 1926.—*D'Erasmo, G.*, Fauna dei calcari a ittioliti di Pietraroia. Palaeont. Italica, vol. xxi., p. 59, 1915.—Catalogo dei pesci delle Tre Venezie. Mem. Istit. R. Univ. Padova, vol. vi., 1922.—*Eastman, C. R.*, Les Types de poissons fossiles du Monte Bolca. Mém. Soc. Géol. France, vol. xiii., no. 34, 1905.—Devonic Fishes of the New York Formations. Mem. New York State Mus., Albany, no. 10, 1907.—Devonian Fishes of Iowa. Ann. Rep. Iowa Geol. Surv., 1907 (1908).—Catalogue of Fossil Fishes in the

Scales.—Louis Agassiz distinguished four kinds of scales, to which in his system there correspond as many Orders.

1. *Placoid scales* occur only among the Elasmobranchs. They are usually small rhombic plates, star-shaped, leaf-shaped, pointed, spade-shaped, or

Carnegie Museum. Parts I.-IV. Mem. Carnegie Mus., Pittsburgh, vol. iv., no. 7, 1911 ; vol. vi., nos. 5, 6, 7, 1914—Fossil Fishes in the Collection of the United States National Museum. Proc. U.S. Nat. Mus., vol. 52, no. 2177, 1917.—*Fowler, H. W.*, Fossil Fish Remains of the Cretaceous, Eocene and Miocene Formations of New Jersey. Bull. 4, Geol. Surv. New Jersey, 1911.—*Goodrich, E. S.*, Dermal Fin-rays of Fishes. Quart. Journ. Micro. Sci., vol. 47, p. 465, 1904.—Development, Structure, and Origin of Median and Paired Fins of Fish. *Loc. cit.*, vol. 50, p. 333, 1906.—Scales of Fish. Proc. Zool. Soc., 1907, p. 751. 1908.—Vertebrata Craniata (Cyclostomes and Fishes), in Lankester's Treatise on Zoology, part IX., 1909.—*Günther, A.*, An Introduction to the Study of Fishes. Edinburgh, 1880.—*Hay, O. P.*, Upper Cretaceous Fishes from Mount Lebanon, Syria. Bull. Amer. Mus. Nat. Hist., vol. xix., art. x., 1903.—*Heckel, J. J.*, Beiträge zur Kenntniss der fossilen Fische Österreichs. 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Belg., vol. ii., 1902.—Les Poissons éocènes. *Loc. cit.*, vol. iii., 1905.—Les Poissons oligocènes. *Loc. cit.*, vol. v., 1910.—Les Poissons néogènes. *Loc. cit.*, Mém. no. 32, 1926.—Poissons fossiles du Nord de la France. Mém. Soc. Géol. Nord, vol. v., no. 1, 1906.—Notes sur la paléontologie du Congo. Revue Zool. Africaine, vol. viii., p. 67, 1920.—Poissons de la Molasse suisse. Mém. Soc. Paléont. Suisse, vols. xlvi., xlvii., 1927. —Les Poissons du Crétacé marin de la Belgique. Bull. Soc. Belge Géol., etc., vol. xxxvii., p. 199, 1929.—*Müller, J.*, Über den Bau und die Grenzen der Ganoiden und über das natürliche System der Fische. Abhandl. Akad. Wiss., Berlin, 1844, p. 117. Translated in Taylor's Scientific Memoirs, vol. iv.—*Newberry, J. S.*, The Palaeozoic Fishes of North America. Mon. U.S. Geol. Surv., no. xvi., 1889 (1890).—*Oertle, G. F.*, Das Vorkommen von Fischen in der Trias Württembergs. Neues Jahrb. f. Min., etc. Beil.-Bd. lx., Abt. B., p. 325, 1928.—*Pictet, F. 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H.*, Extinct Vertebrata of the Moray Firth Area. In *Harvie-Brown* and *Buckley's* Vertebrate Fauna of the Moray Basin (Edinburgh, 1896) ; supplement in Proc. Roy. Phys. Soc. Edinb., vol. xiii., p. 376, 1897.—*Volta, G. S.*, Ittiolitologia veronese. 2 vols. Verona, 1796, 1809.—*Weiler, W.*, Beiträge zur Kenntnis der tertiären Fische des Mainzer Beckens. Abhandl. Hess. Geol. Landesanst. Darmstadt, vol. vi., p. 67, 1922 ; vol. viii., pt. 3, p. 1, 1928.—Fischreste aus dem nubischen Sandstein und aus den Phosphaten Oberägyptens und der Oase Baharije. Abhandl. Bay. Akad. Wiss., Math.-naturw. Abt., n.s. 7, p. 12, 1930.—*Weiler, W.*, and *Krejci, K.*, Fische aus dem rumänischen Tertiär. Senckenbergiana (Frankfurt), vol. x., p. 55, 1928.—*White, E. I.*, Eocene Fishes from Nigeria. Bull. Geol. Surv. Nigeria, no. 10, 1926.—Vertebrate Faunas of the English Eocene, vol. i. British Museum, 1931.—*Williamson, W. C.*, Microscopic Structure of

even conical structures which lie close together and form a rough mosaic (shagreen). The placoid scales are often of variable form on different parts of the body, and sometimes (*e.g.* among the rays) single tubercles are conspicuous by their large size and sculpture, and appear as thick plates externally roughened or provided with spines. Placoid scales (Figs. 1-3)

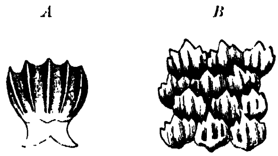


FIG. 1.

A, Scale of *Scyllium canicula*. Recent. $^{50}/_{1}$. *B*, Scales of *Carcharias* (*Prionodon*) *gangeticus*. Recent. Magnified.

FIG. 2.

Large placoid scale of *Raja antiqua*, with spine. Pliocene. Nat. size.

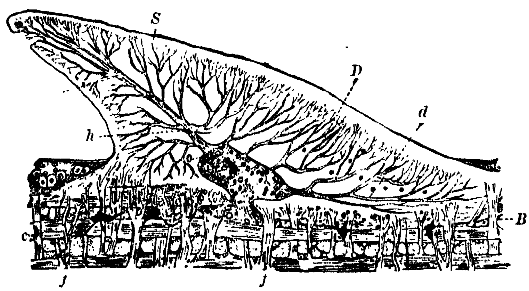


FIG. 3.

Sagittal section through a scale of *Scymnus lichia*. Recent. $^{60}/_{1}$. *B*, basal plate; *D*, dentine; *S*, enamel; *c*, cutis; *d*, horizontal dentine canals; *f*, bundles of connective tissue; *h*, large principal dentine canal extending upwards; *o*, odontoblasts; *p*, pulp cavity (after O. Hertwig).

have the structure of teeth and consist of a basal plate (of thick phosphate of lime) penetrated by vertical bundles of connective tissue fibres sunk in the skin, and a freely projecting upper part composed of dentine and penetrated by coarser and finer little canals (*vasodentine*). All the canals arise from a cavity (*pulpa*, *p*) filled with connective tissue and tooth cells (*odontoblasts*, *o*), and subdivide outwards into continually finer branches. Besides phosphate of lime the dentine comprises small quantities of fluoride and carbonate of lime. The core of dentine is covered by a thin, shining, very hard structureless outer layer (*ganodentine* or *vitrodentine*), which corre-

the Scales and Dermal Teeth of some Ganoid and Placoid Fishes. Phil. Trans. Roy. Soc., 1849, p. 435; also 1851, p. 643.—*Woodward, A. S.*, Catalogue of Fossil Fishes in the British Museum. Parts I.-IV., 1889–1901.—Fossil Fishes of the Hawkesbury Series at Gosford. Mem. Geol. Surv., N.S. Wales, Palaeont., no. 4, 1890.—Fossil Fishes of the Talbragar Beds. *Loc. cit.*, no. 9, 1895.—Fossil Fishes of the Hawkesbury Series at St. Peter's. *Loc. cit.*, no. 10, 1908.—A Carboniferous Fish Fauna from the Mansfield District, Victoria. Mem. Nat. Mus., Melbourne, no. 1, 1906.—Fossil Fishes of English Chalk. Mon. Palaeont. Soc., 1902–12.—Use of Fossil Fishes in Stratigraphical Geology. Quart. Journ. Geol. Soc., vol. lxxi., p. lxii, 1915.—Fossil Fishes of English Wealden and Purbeck Formations. Mon. Palaeont. Soc., 1916–19.—Presidential Addresses to the Linnean Society of London. Proc. Linn. Soc. Lond., Sess. 132-134, 1920–22.—Fish-Remains from the Upper Old Red Sandstone of Granite Harbour, Antarctica. Brit. Antarct. (Terra Nova) Exped., Nat. Hist. Rep., vol. i., no. 2, 1921.—*Yabe, H.*, and *Obata, T.*, Some Fossil Fishes from the Cretaceous of Japan. Japanese Journ. Geol. Geogr., vol. viii., p. 1, 1930.

sponds histologically and chemically with the enamel of teeth. Placoid scales often fall out and are replaced like teeth by successional tubercles.

2. *Ganoid scales* (Figs. 4-7) attain a larger size than placoid, and usually cover the whole trunk. They are of rhombic or rounded shape, and in the latter case overlap one another like roofing tiles. Those of rhombic form are usually arranged in regular rows, and are movably articulated by a tooth-like process of the upper margin which fits into a corresponding hollow on the inner side of the adjoining scale. The exposed outer face is covered by an enamel layer (*ganoine*); it is usually thick and shining, smooth, rugose, or ridged, and beneath it there is a basal plate consisting of bone substance and pierced by numerous canals. Among the Palaeozoic genera, indeed, the basal plate shows great complexity (Fig. 7). The deepest layer is laminated, with the elongated bone lacunae between the layers (*isopedin*). The middle layer has irregularly arranged bone lacunae, and is traversed by large anastomosing vascular canals. In most *Crossopterygii* the outer layer immediately below the ganoine consists of tubercles or ridges of hard dentine, each with its own pulp cavity from which fine tubules radiate (*cosmine*). In the *Chondrostei* this cosmine layer is reduced, while the overlying ganoine becomes thickened in concentric layers.

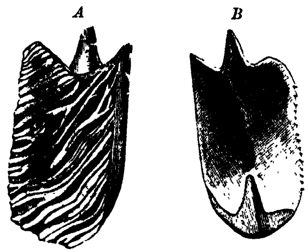


FIG. 4.

Scale of *Elonichthys* (*Cosmoptychius*) *striatus* Ag. sp. Outer (*A*) and inner (*B*) aspects. Lower Carboniferous. $^3/_1$.

FIG. 5.

Two scales of *Polypterus bichir* Bonap. Recent. Inner aspect. Nat. size.

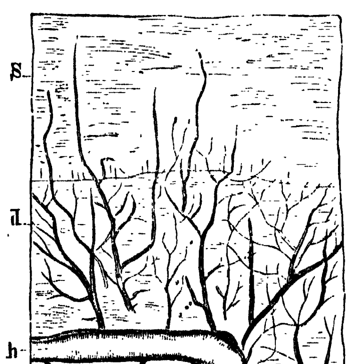


FIG. 6.

Vertical section of a scale of *Lepidosteus*. Recent. *S*, enamel (*ganoine*); *d*, dentine tubules; *h*, vascular canal. $^{300}/_1$ (after O. Hertwig).

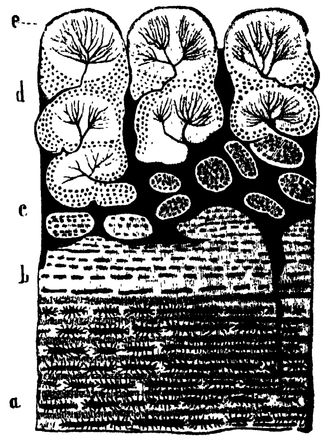


FIG. 7.

Vertical section of a scale of *Holoptychius*, highly magnified. Devonian. *a*, *b*, laminated layer with spindle-shaped bone lacunae (*isopedin*); *c*, bony layer with large vascular canals; *d*, layer with fine, branching dentine tubules (*cosmine*); *e*, enamel (*ganoine*) (after Pander).

In the later Ganoids the cosmine layer disappears, and the laminated ganoine alone remains.

3. *Cycloid and ctenoid scales* are exactly alike in general characters, being thin, elastic, and of rounded, elliptical, four-, five-, or six-sided shape. They consist of a homogeneous, transparent shining surface-layer of phosphate of lime, and of a base of connective tissue deficient in alkalies. The scales are developed in special folds of the cutis, and generally overlap one another like roofing tiles. Cycloid scales (Fig. 8, *A-C*) generally exhibit a rounded or oval form and a simple non-serrated hinder border. In ctenoid scales (Fig. 8, *D*, *E*) there project from the hinder border small points and denticles, which are sometimes arranged in several series one behind the other, and may indeed cover a considerable part of the hinder surface and have the same structure as the superficial layer. From the so-called primitive field divergent lines radiate chiefly forwards and backwards, and sometimes also pass into reticulations; these lines being merely fissure-like interruptions in the outer layer (Fig. 9). Between the upper parallel layers of the fibrous connective tissue of the base there are often intercalated small, round, concentrically marked calcareous bodies, which are most numerous beneath the primitive field, sometimes fused with each other into a continuous layer, and here and there exhibit bone cells. Such scales are not essentially different from very thin ganoid scales.

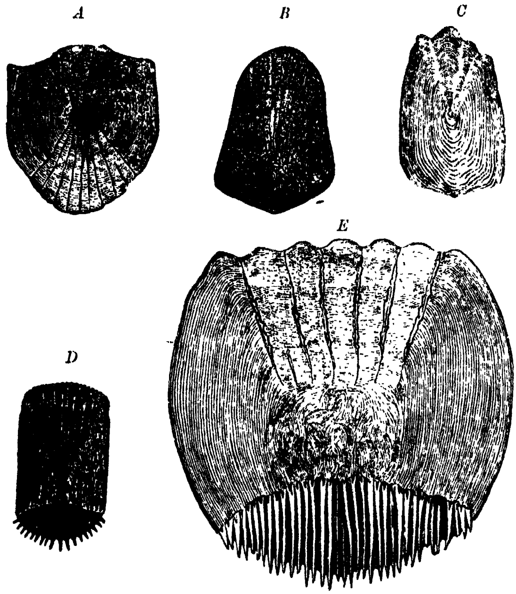


FIG. 8.
Cycloid scales of *A*, *Leuciscus*, *B*, *Mormyrus*, and *C*, *Naucrates*. Ctenoid scales of *D*, *Solea*, and *E*, *Holacanthus*. Much magnified.

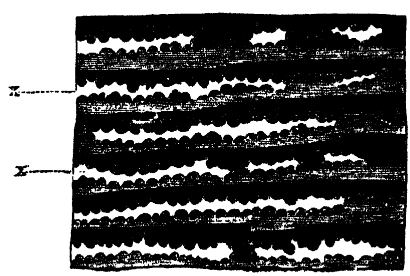


FIG. 9.
External surface of a scale of *Pleuronectes*, to show the vacuities (*x*) between the raised concentric lines. Very much magnified (after Baudelot).

The large plates, shields, spines, etc., which partly cover the body and partly the head of many fishes (*Arthrodira*, *Siluridae*, *Acipenseridae*), consist either of uniform bone substance, or, like the ganoid scales, of layers of bone, dentine (cosmine), and enamel (ganoine).

Large spines (*Ichthyodorulites*) (Fig. 10), sometimes occur on the front margin of the median, and more rarely of paired fins, or on the head of cartilaginous fishes (*Elasmobranchii*). They are usually implanted loosely in

the muscles by an elongated base, only exceptionally (*Chimaera*) articulated with a lower piece. Like the scales and teeth of Placoid fishes they consist entirely of varieties of dentine. Ichthyodorulites often attain a remarkable size, and occur isolated in a fossil state, while the Palaeozoic examples are sometimes characterised by a rich sculpturing.

The outer projecting parts of the fins are also to be regarded as dermal structures. They arise as folds of skin, which gradually become strengthened by numerous horny fibres (*ceratotrichia* or *actinotrichia*) (*Elasmobranchii*, *Dipnoi*). In most Ganoids and Teleosteans these fibres are replaced by bony rays (*lepidotrichia*), which seem to originate in rows of scales placed end to end and so consist of two closely apposed halves. In the *Acanthopterygii* (Fig. 11) each half of every spinous ray consists of a single piece; in the lower fishes all the rays are subdivided by transverse sutures into numerous little pieces and often branch towards the end. Spiny and articulated rays frequently occur in one and the same fin, and in this case the spines are always in front. The rays of the unpaired fins are borne as a rule on flat cartilaginous or bony supports with which they articulate (Fig. 11, *C*). These fin supports in the most primitive fishes are correlated with the neural and haemal arches and in direct line with them, each consisting of a proximal piece (*axonost*) and a distal piece (*baseost*). In the higher fishes they penetrate between the spinous processes of the vertebrae and are known as *interspinous bones* or, according to their position, as *interneurals* and *interhaemals*.

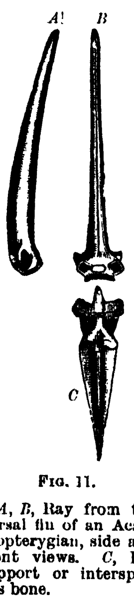


FIG. 11.

A, *B*, Ray from the dorsal fin of an Acanthopterygian, side and front views. *C*, Fin support or interspinous bone.

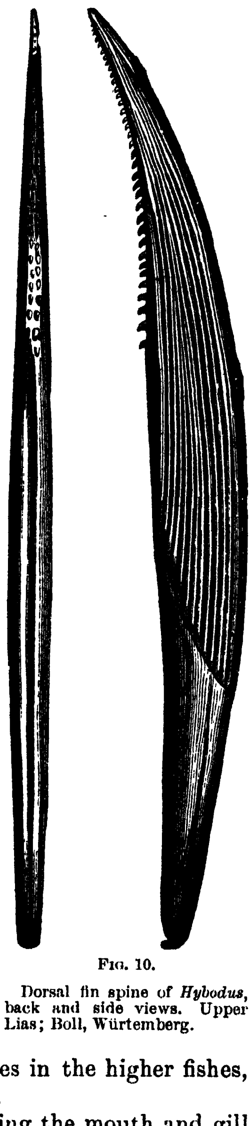


FIG. 10.

Dorsal fin spine of *Hybodus*, back and side views. Upper Lias; Boll, Würtemberg.

In many Elasmobranchs (*Pristiophorus*, *Raja*) every gradation can be observed between the Placoid scales of the external skin and the teeth; and as both exhibit essentially the same histological structure, while the teeth only assume a firm connection with the head bones in the higher fishes, the teeth must indeed be regarded as dermal structures.

Among fishes all the cartilages or bones surrounding the mouth and gill cavity may bear teeth. These originate in the calcification of skin papillae, consisting of a crown which freely projects, and of a root which is surrounded with connective tissue or united with the head bones. Their form and proportions are extraordinarily variable according to their functions. All gradations exist from the minute granular denticles of the perch to the long

brush-like teeth of the sheat-fish, to the robust prehensile teeth of the pike, and the powerful conical or laniary teeth of *Dendrodus* or *Portheus*. Among the sharks there often occur teeth shaped like an arrow-head, flattened on one side, with or without lateral denticles. To crush the food there are sometimes obtusely conical teeth, sometimes bean-shaped, hemispherical, or pavement-like teeth, and in certain Elasmobranchs the teeth are closely pressed together into a continuous mosaic. Peculiar cutting dental plates of considerable size occur in *Diodon*, *Arthrodira*, and *Chimaera*.

The number of the teeth in fishes is as varied as their shape. While the *Dipnoi*, *Holocephali*, and Gymnodonts possess only four to six teeth in all, in many sharks and teleosteans these are numbered by hundreds.

In the young of almost all fishes the teeth are fixed to the cartilaginous or bony support by fibrous connective tissue, and in sharks and in many bony fishes this arrangement persists throughout life, so that after long maceration the teeth can easily be stripped off their base. In bony fishes and many ganoids the roots of the teeth become fused with the bone, and a socket-like elevation usually grows round the teeth. Exceptionally, teeth are also implanted in distinct sockets. The successional teeth are usually developed by the side of the functional teeth and continually push them out.

With few exceptions the crown of the tooth consists of dentine (cosmine), vasodentine, and ganodentine (*ganoine* or enamel), the root of vasodentine or osteodentine. The enamel forms a thin, brilliant, homogeneous superficial layer, as hard as glass, and is easily recognised in polarised light by its double refraction. Very fine unbranched tubules frequently pass from the dentine into the enamel. It is composed of phosphate of lime, with a little fluoride of lime, a little carbonate of lime, phosphate of magnesia, and a very small quantity of organic matter. The dentine or tooth substance contains no fluoride of lime but much more organic matter than the enamel, is less hard, and dissolves more slowly in acids. Typical dentine or cosmine (Fig. 12, *D*) is traversed by very fine outwardly branching tubules, which radiate outwards from the pulp or its branches, and contain thread-like processes of the tooth cells (*odontoblasts*). The dentine is also very frequently traversed by large anastomosing canals (*Haversian canals*), in which blood-vessels penetrate, and the walls of which are covered with odontoblasts. Fine dentine tubules then radiate in a peripheral direction from these large canals. This vascular modification of tooth substance is known as *vasodentine* (Figs. 13, 14, *VD*).

The root of the teeth of fishes is distinguished from the crown by the absence of an enamel layer. It consists either entirely of vasodentine, or also exhibits bone cells with radiating primitive tubules (*osteodentine*).

The internal skeleton of fishes shows that in the different Orders of this Class there persist until adult life almost all the stages of development which are only temporary among the higher Vertebrates. The whole process of the gradual segmentation, chondrification, and ossification of the vertebral column and of the rest of the skeleton is quite clear in the different groups of fishes, and the fossil forms from the Palaeozoic and Mesozoic deposits furnish the most important information in this respect.

Vertebral Column.—The first trace of the internal skeleton in all Vertebrata is confined to an elastic rod-like structure (*chorda dorsalis* or *notochord*) extending longitudinally on the dorsal side of the body, consisting of oil-bearing

cells, and enveloped in a laminated sheath. Upon the chorda dorsalis lies the spinal chord; below it, the ventral cavity of the body.

The vertebral column persists throughout life in this primitive stage only in *Amphioxus*. The notochord, indeed, still remains unsegmented in the Cyclostomes, but the spinal chord is already protected by arch-shaped bars of cartilage developed round the sheath of the notochord (neural arches); and at the front end there is developed a cartilaginous capsule for the reception of the brain.

In all typical fishes the vertebral axis is divided into ring-shaped segments (vertebrae), which are partly or completely cartilaginous or bony. The chondri-

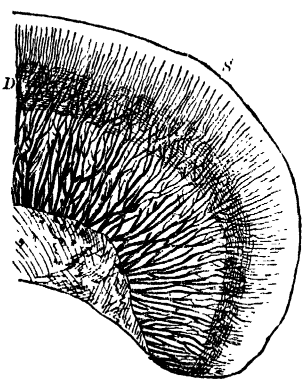


FIG. 12.

Vertical section of a tooth of *Lepidotus* (*Sphaerodus*) *gigas* Ag. Consisting of dentine (*D*) and enamel (*S*). Upper Jurassic. Much magnified.

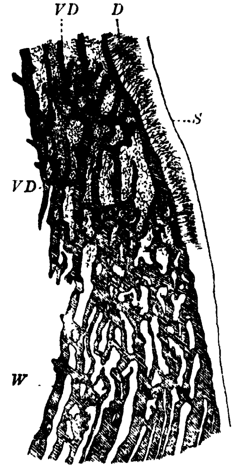


FIG. 13.

Vertical section of part of a tooth of a pike (*Esox*). Recent. *D*, dentine; *S*, enamel; *VD*, vasodentine; *W*, root of tooth. Much magnified (after Sternberg).

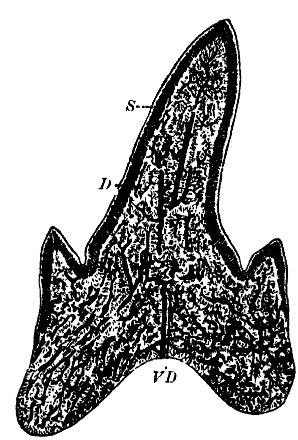


FIG. 14.

Vertical section of a tooth of *Lamna*. Eocene. *D*, dentine; *S*, enamel; *VD*, vasodentine. Much magnified.

fication or ossification always arises in the skeletogenous layer bounding the notochordal sheath, and begins with the upper and lower arches.

A complete vertebra consists of a vertebral body (*centrum*) surrounding the notochord, two upper half-arches surrounding the neural canal (*neurapophyses*), and two lower half-arches (*haemapophyses*). The upper arches are united with a dorsal spinous process (*processus spinosus, spina dorsalis,* or *neural spine*), while the lower arches either unite in the caudal region into a ventral spinous process (*spina ventralis*), or remain as lower transverse processes (*parapophyses*).

In many fishes provided with a cartilaginous vertebral column (Selachians and Acipenseroids), there are interposed between the upper and lower arches cartilaginous intercalary pieces (*intercalaria*) which sometimes exceed the arches in size (Figs. 16, 17, *i*).

The *vertebral centra* or vertebral bodies in cartilaginous fishes usually surround a persistent remnant of the notochord, which pierces the whole of the vertebral column and partly fills the intervertebral spaces. The cartilaginous, calcified, or bony anterior and posterior faces of the vertebral bodies

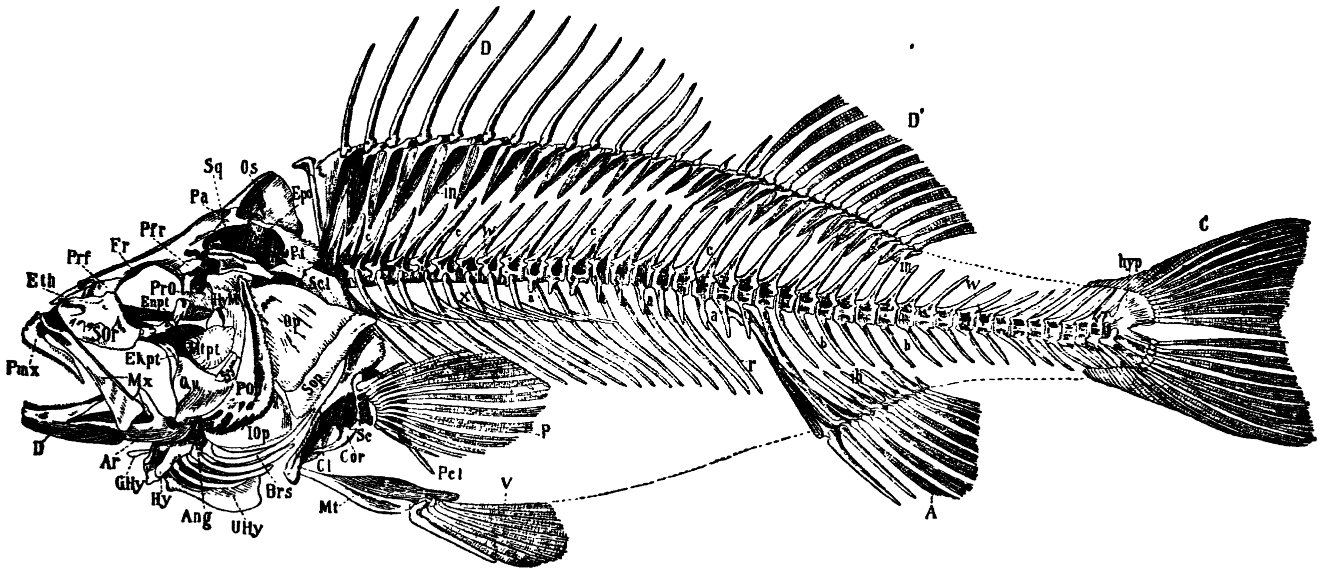


FIG. 15. Skeleton of Perch (*Perca fluviatilis*).

I. ***Head.***—***Ang***, angular; ***Ar***, articular; ***Brs***, branchiostegal rays; *D*, dentary; *Ekpt*, ectopterygoid; *Enpt*, entopterygoid; *EpO*, epiotic; *Eth*, ethmoid; *Fr*, frontal; ***GHy***, glossohyal; ***Hy***, ceratohyal; ***HyM***, hyomandibular; *IOp*, interoperculum; *Mtpt*, metapterygoid; *Mx*, maxilla; *Op*, operculum; ***Os***, supraoccipital; *Pa*, parietal; ***Pfr***, postfrontal; *Pmx*, premaxilla; ***POp***, preoperculum; ***Prf***, prefrontal; *PrO*, prootic; *Qu*, quadrate; *Sop*, suboperculum; *SOr*, suborbitals; *Sq*, squamosal; *Sy*, symplectic; ***UHy***, urohyal.

II. ***Vertebral Column.***—*a*, parapophyses; ***b***, haemapophyses; *c*, neurapophyses; *r*, ribs; *w*, vertebral centra; *x*, intermuscular bones.

III. ***Appendages.***—***A***, anal fin; *C*, caudal fin; *Cl*, cleithrum; *Cor*, coracoid; *D*, *D'*, two dorsal fins; *hyp*, hypural; *ih*, interhaemals; *in*, interneurals; *Mt*, pelvic fin support; ***P***, pectoral fin; *Pcl*, postcleithrum; *Pt*, post temporal; *Sc*, scapula; *Scl*, supracleithrum; *V*, pelvic fin.

are deeply hollowed like double cones (*amphicoelous*), and thus give the centrum an hour-glass shape. In the *Elasmobranchii* there is usually a partial calcification, in the *Ganoidei* and *Teleostei* an ossification of the primitive cartilaginous centrum. While, however, the bony fishes generally exhibit complete ossification of the whole vertebra with all its processes, the Ganoids of the Palaeozoic and Mesozoic deposits display every possible stage in the process of ossification. In completely ossified vertebrae the anterior and posterior edges of the amphicoelous centra are in close contact and also bound together by ligaments: the notochord persists only in the intervertebral spaces, and does not form a continuous thread. The arches are firmly fused with the

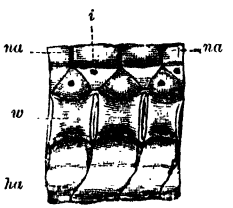


FIG. 16.
Three caudal vertebrae of *Centrophorus* in side view. *ha*, haemal arches; *i*, intercalary cartilages; *na*, neural arches; *w*, vertebral centra (after Hasse).

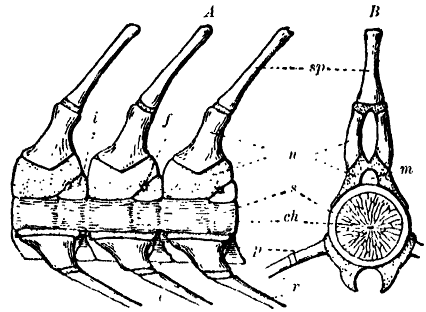


FIG. 17.
Vertebrae from the abdominal region of the Sturgeon (*Acipenser*), in side view (*A*) and in vertical transverse section (*B*). Cartilage dotted, bone white. *c*, ventral intercalary pieces; *ch*, notochord; *f*, nerve foramina; *i*, intercalary pieces; *m*, neural canal; *n*, neural arches; *p*, parapophyses; *r*, ribs; *s*, sheath of notochord; *sp*, neural spines (after R. Hertwig).

centrum, and on the anterior margin of the upper arches there usually projects a short process (*zygapophysis*), which overlaps a similar posterior process of the centrum on each side, and thus strengthens the union of contiguous vertebrae (Fig. 18). In the hinder or caudal region the lower arches form a ventral spinous process (Fig. 18); in the anterior or abdominal region the lower arches project as short parapophyses, and serve as supports for the movable ribs. True transverse processes (*diapophyses, processus transversi*), to which the ribs are attached in the higher Vertebrata, and which arise from the upper arches, occur only exceptionally (*Polypterus, Pleuronectes*) besides the parapophyses. In the Cyclostomes and Chimaeras ribs are entirely absent; in the *Elasmobranchii* and cartilaginous Ganoids they are usually feebly developed or rudimentary. The ribs of the two sides are never united with each other at the ventral border either directly or through the intervention of a sternum. The *intermuscular bones*, which arise in the membrane between the muscle plates, must not be confounded with ribs; they are delicate bony filaments, often forked at one end, which are disposed between the muscles, and rest on the vertebral centra, arches, or ribs.

The number of the vertebrae in fishes varies most remarkably in the different groups. In certain bony fishes (*Ostracion*) only 15 are to be counted, while in others there are 70 to 80, in the eel about 200, in many sharks from 350 to 400.

The hinder end of the vertebral column in the embryonic stage of all

fishes is *diphycercal* or *heterocercal*.[1] In the first case the vertebral column extends in a straight line to the end of the trunk, and is symmetrically fringed above and below with the caudal fin. The *Cyclostomi*, *Dipnoi*, and many *Crossopterygii* (Fig. 19) either remain in this embryonic stage throughout life, or revert to it by acquiring a secondarily developed diphycercal (or *gephyrocercal*) tail. In the *heterocercal* fishes (sharks, rays, etc., and many Ganoids) the end of the vertebral column is bent upwards (rarely downwards —*hypocercal*), and completely passes into the upper (rarely lower) lobe of the caudal fin, which is usually elongated, and exceeds the lower (rarely upper) lobe in size (Fig. 20). Between the diphycercal and heterocercal types of tail there are many gradations. In the *hetero-diphycercal* tail the vertebral column

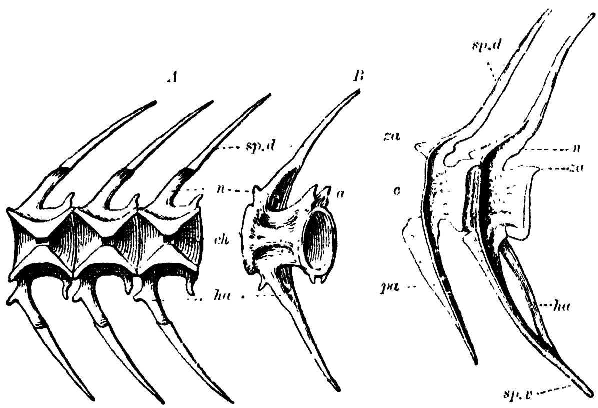


FIG. 18.

Caudal vertebrae of the Carp. *A*, Vertical longitudinal section of three vertebrae. *B*, Detached vertebra, chiefly in side view. *C*, Last abdominal and first caudal vertebra. *c*, centrum; *ch*, notochord; *ha*, haemal arches; *n*, neural arches; *pa*, parapophysis; *sp.d*, neural spines; *sp.v*, haemal spines; *za*, zygapophyses (after R. Hertwig).

is elongated in a gentle upward curve at its hinder end, and fringed above and below with fin rays; but the rays of the upper lobe are much less developed than those of the lower lobe. Sometimes also the external caudal fin consists of two similar lobes, while the vertebral column is bent upwards, and extends far into the upper lobe (Fig. 21). Such fins are externally *homocercal*, internally heterocercal. In the *hemi-heterocercal* tail the upper lobe of the externally symmetrical caudal fin is still partly or completely covered with scales.

In all cycloid and ctenoid fishes the caudal fin is at least externally *homocercal* (Fig. 22). The vertebral column terminates in front of the fin with a vertebra bearing a broad, vertical, fan-shaped plate (*hypural*), which is formed by the fusion of several fin supports and haemapophyses. This terminal plate generally encloses a short, upwardly directed remnant of the

[1] *Agassiz, A.*, Young Stages of Osseous Fishes. I. Development of the Tail. Proc. Amer. Acad. Arts Sci., vol. xiii., p. 117, 1878.—*Huxley, T. H.*, Development of some parts of the Skeleton of Fishes. I. Tail in Teleostean Fishes. Microsc. Journ., vol. vii., p. 33, 1859.—*Kölliker, A.*, Über das Ende der Wirbelsäule der Ganoiden und einiger Teleostier. Leipzig, 1860. —*Ryder, J. A.*, Origin of Heterocercy and the Evolution of the Fins and Fin-rays of Fishes. Ann. Rep. Commiss. Fish and Fisheries for 1884, Washington, p. 981, 1886. See also *Goodrich, E. S.*, 1906, ref. in footnote, p. 3.

notochord or a bony style (*urostyle*). There is thus an internal heterocercy as the basis of the homocercal tail.

Nearly all Palaeozoic fishes have a diphycercal (perhaps gephyrocercal) or heterocercal tail; hemi-heterocercal forms begin with *Acentrophorus* in the

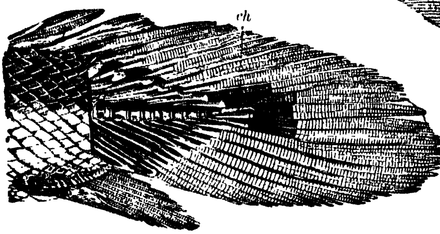


FIG. 19.

Diphycercal (or gephyrocercal) caudal fin of *Polypterus bichir* Bonap. Recent. *ch*, hinder end of vertebral column (after Kölliker).

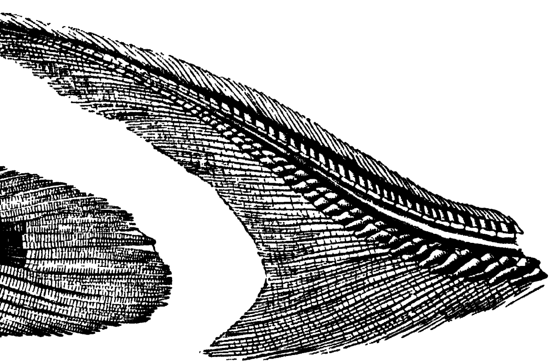


FIG. 20.

Externally and internally heterocercal caudal fin of the Sturgeon (*Acipenser*).

Upper Permian, and are common in the Triassic and Jurassic. The Cretaceous, Tertiary, and Recent bony fishes, when adult, exhibit a homocercal tail; but in their immature condition there is always a diphycercal or heterocercal stage.

Skull.—The head forms the anterior end of the vertebral axis, and its skeleton

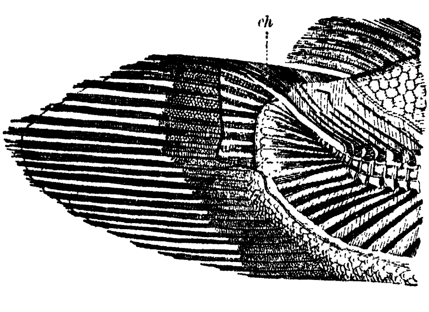


FIG. 21.

Internally heterocercal caudal fin of *Amia*. Recent. *ch*, cartilaginous hinder end of the vertebral column, with rudiment of notochord (after Kölliker).

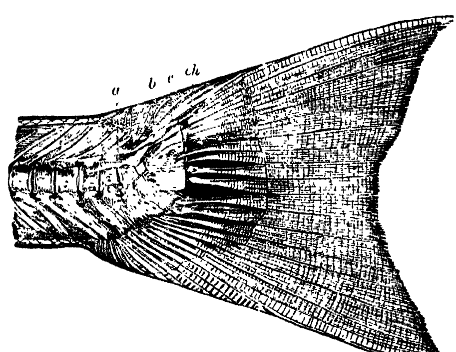


FIG. 22.

Externally homocercal (stegurous) caudal fin of the Salmon (*Salmo salar*). *a*, *b*, *c*, upper roofing bones of the end of the notochord; *ch*, projecting end of the notochord (after Kölliker).

exhibits a greater complexity in fishes than in the higher Vertebrates. Except in *Amphioxus*, the brain is enclosed in a cartilaginous or bony capsule, the skull or cranium, which also contains the organs of hearing, sight, and smell. With the skull are connected a large number of paired cartilaginous or bony pieces, which together form the so-called *visceral skeleton*.

The embryonic primordial cranium of all Vertebrates is cartilaginous, and

is developed like the vertebral column round the notochord, which always extends far into the base of the skull.

In the typical *Elasmobranchii*[1] (Fig. 23) the whole cranial skeleton is cartilaginous, and only exceptionally hardened by the deposition of phosphate of lime (*Ichthyotomi*). The long cranial capsule does not exhibit any sutures, and comprises in its anterior part (ethmoidal region) the olfactory nerves, in the middle (orbital region) the optic nerves and eyes, in the hinder part the organs of hearing, the hemispheres of the cerebrum, and the cerebellum. The visceral skeleton consists of a number of variously shaped cartilaginous arches, of which the foremost (pterygoquadrate) surrounds the cleft of the mouth, and is characterised by its relatively large size. The mandible or lower jaw is articulated with the pterygoquadrates. Two small labial cartilages, sometimes termed maxilla and premaxilla, occur on each side in front of

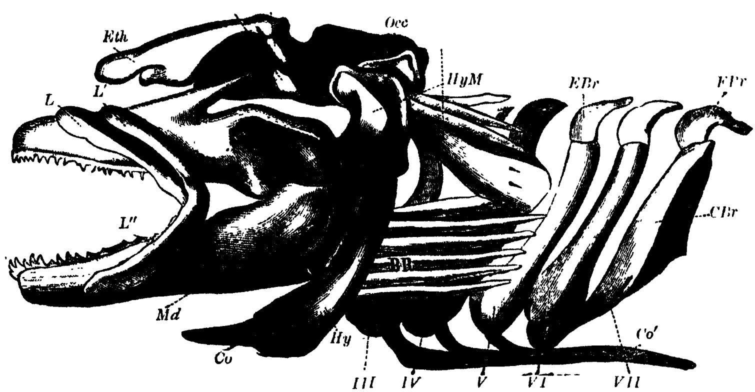


FIG. 23.

Skull and branchial apparatus of *Squatina vulgaris* Risso. Recent. *BR*, rays of the hyoid arch; *CBr*, ceratobranchial; *Co*, copula of the hyoid arch; *C'o'*, hindmost copula of the branchial arches; *EBr*, epibranchial; *Eth*, ethmoidal region; *Hy*, hyoid arch; *HyM*, hyomandibular; *L*, *L'*, *L''*, anterior (premaxillary), posterior (maxillary), and inferior (premandibular) labial cartilages; *Md*, lower jaw or mandible; *Occ*, occipital region. *III-VII*, Branchial arches (after Gegenbaur).

and below the pterygoquadrate. The latter element is connected with the skull in the ethmoidal region by ligament, and in the hinder portion by the second visceral arch, of which the upper portion (hyomandibular) is in contact with the auditory region of the skull, while the lower portion forms the hyoid arch. The pterygoquadrate and mandible are provided with teeth. Behind the hyoid arch there follow five (rarely six or seven) other visceral arches, which serve for the support of the respiratory organs, are composed of several pieces, and united ventrally by median intercalary pieces (copulae). Both the gill arches and the hyoid bear cartilaginous gill rays. In the *Holocephali* the pterygoquadrate and hyomandibular fuse together and with the cranial capsule. The mandible thus becomes *autostylic*, *i.e.* articulates directly with the cranium.

In the cartilaginous ganoids (*Acipenser*, *Spatularia*), bony elements begin to take part in the formation of the head. The cranial capsule, indeed, remains for the most part cartilaginous; but externally there are a number of bony plates, which cover the cranium on the top and sides, and there

[1] *Gegenbaur, C.*, Das Kopfskelet der Selachier. Leipzig, 1872.

is also developed below the base of the skull a long, delicate, dermal bone (parasphenoid), which extends forwards to the ethmoidal region and backwards even beyond the occiput. The pterygoquadrate, hyomandibular, and mandible are also covered with bone; and the fold of skin covering the gill clefts is likewise ossified as a single gill cover (operculum). The pterygoquadrate and hyomandibular form the freely movable (*hyostylic*) supports of the mandible.

The *Dipnoi* resemble the cartilaginous ganoids, except that in them the pterygoquadrate and hyomandibular are fused with the cranium (autostylic).

In the scaly ganoids and bony fishes more or less ossification of the cranial capsule and visceral skeleton occurs. The ossification begins first, as in the cartilaginous ganoids, with dermal bones, and then the substitution of bony substance for cartilage follows. The distinction between dermal bones and ossified cartilage (cartilage bones) can, however, only be made by determining their mode of development.

In the cranium proper (Fig. 24) three regions are distinguishable—the occipital portion, the auditory, and the orbito-ethmoidal regions. The hindmost or occipital region consists of four cartilage bones:—(1) The lower occipital bone (occipitale basilare, basioccipital), which usually contains a persistent remnant of the notochord, and is in contact with the vertebral column with its deeply hollowed hinder end; (2, 3) a right and left lateral occipital (occipitalia lateralia, exoccipitals), which bound the greater part of the foramen magnum; and (4) an upper occipital (occipitale superius, supraoccipital) which belongs to the cranial roof, often thrust between the parietal bones and provided with a vertical median crest.

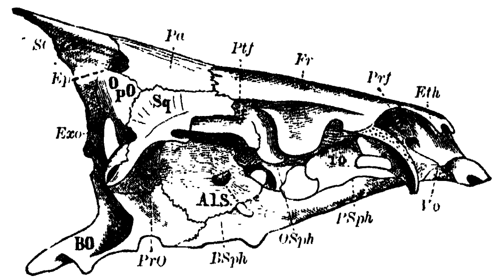


FIG. 24.

Cranium of the Carp (*Cyprinus carpio* Linn.) *AlS*, alisphenoid; *BO*, basioccipital; *BSph*, basisphenoid; *Ep*, epiotic; *Eth*, ethmoid; *Exo*, exoccipital; *Fr*, frontal; *io*, interorbital; *OpO*, opisthotic; *OSph*, orbitosphenoid; *Pa*, parietal; *Prf*, prefrontal; *PrO*, proötic; *PSph*, parasphenoid; *Ptf*, postfrontal; *SO*, supraoccipital; *Sq*, squamosal; *Vo*, vomer (after R. Owen).

The auditory capsules are surrounded laterally by several pairs of bones often completely covered by the facial and other membrane bones. Among them are distinguished immediately in front of the exoccipitals the opisthotic (*OpO*), the epiotic (*Ep*), adjoining the latter in its hinder upper part, and the proötic (*PrO*), which is usually pierced by the trigeminal nerve. With these bones, which form the auditory capsule proper, there is connected a cartilage bone on each side above and in front of the opisthotic, the pterotic, which is overlaid by a membrane bone, the squamosal, and usually in the higher fishes fused with the latter. The mandibular suspensorium (hyomandibular) articulates with the lower face of the pterotic.

The lateral investment of the middle orbital region of the skull, which sometimes remains cartilaginous or membranous, and is sometimes more or less completely ossified, consists externally of facial bones. Two pairs of bones can be distinguished here, posteriorly the alisphenoid placed just in front of the proötic, and anteriorly the orbitosphenoid; both pairs, but especially the orbitosphenoids, often fuse together completely in the middle

line below. The base of the skull is formed by a large dermal bone, the long, sword-shaped parasphenoid, which abuts behind on the basioccipital, in front on the vomer.

The roof of the two hinder regions of the skull only rarely arises in cartilage; it usually consists of membrane bones, which are intimately connected with the cartilage elements. There are thus intercalated between the supraoccipital and the squamosals two parietal bones, and these are followed in front by the two frontal bones, which often fuse together into a large simple plate. By the side of the latter and in front of the squamosal there occurs the postfrontal (sphenotic) cartilage bone, which is overlaid by a membrane bone in the Ganoids, but is exposed in the Teleosteans. There is also occasionally a small supraorbital above the eye.

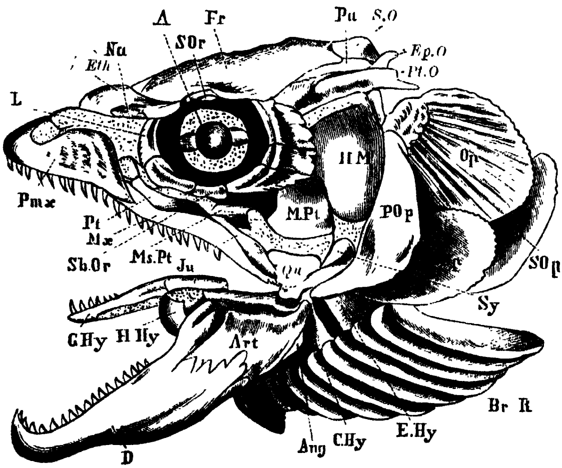


Fig. 25.

Cranial skeleton of the Salmon. The persistent cartilage of the cranium dotted; the bones developed from cartilage lettered in italics, the membrane bones in Roman type. *A*, *eye;* Ang, angular; *Art*, *articular;* Br.R, branchiostegal rays; *C.Hy*, *ceratohyal;* D, dentary; *E.Hy*, *epihyal;* *Ep.O*, *epiotic;* *Eth*, *ethmoid;* Fr. frontal; *G.Hy*, *glossohyal;* *H.hy*, *hypohyal;* *HM*, *hyomandibular;* IOp, interoperculum; Ju, jugal; L, lachrymal; *M.Pt*, *metapterygoid;* *Ms.Pt*, *mesopterygoid;* Mx, maxilla; Na, nasal; Op, operculum; Pa, parietal; Pmx, premaxilla; POp, preoperculum; *Pt*, *palatine;* *Pt.O*, *pterotic* (with squamosal); *Qu*, *quadrate;* *S.O*, *supraoccipital;* Sb.Or, suborbitals; SOp, suboperculum; SOr, supraorbital; *Sy*, *symplectic* (after Parker).

The anterior ethmoidal region possesses as its base the vomer (*Vo*) or ploughshare bone, which also forms the anterior part of the roof of the hard palate. From the vomer on either side there slopes upwards and outwards a prefrontal cartilage bone (*ethmoidale laterale*), which is connected above with the frontal and with the cartilage bone known as ethmoid (*Eth*), which surrounds the nasal capsule above, in front, and partly at the side. One or more small ossifications above each nasal opening, which are sometimes fixed to the outer face of the ethmoid, are termed nasal bones or nasalia (Fig. 25, *Na*).

To the visceral skeleton (Figs. 25, 26) belong the jaw apparatus, the facial bones, and the gill arches. The hyomandibular is in close connection with the hinder part of the pterygoquadrate. Thus arises the so-called suspensorium, which, as support of the mandible, is movably connected by ligaments with the skull. The quadrate articulates below with the mandible, and is firmly fixed above with the symplectic, which occurs at the lower end of the hyomandibular. From the quadrate there extends forwards the angularly bent ectopterygoid, upwards the metapterygoid, and again forwards the mesopterygoid (or entopterygoid), of which the anterior end is connected with the palatine. The latter is fixed by cartilaginous ligaments at its anterior border to the vomer and the ethmoidal region.

In front of the palatine on each side there occur two pairs of rather large

bones, which are usually provided with teeth. The anterior of these, the premaxilla or intermaxilla, usually meets its fellow of the opposite side in a symphysis in front of the ethmoid region. The hinder bone, or maxilla, is sometimes connected with the quadrate through the intervention of a slender jugal or supramaxillary.

The lower jaw (*mandibula*) consists of the articular, a postero-inferior angular, which often remains cartilaginous, and the large principal piece or dentary (*dentale*), which usually bears teeth. On the inner side there is also a membrane bone, the splenial (or *operculare*), which not unfrequently bears teeth, and sometimes (as in the *Crossopterygii*) consists of two or more bony pieces.

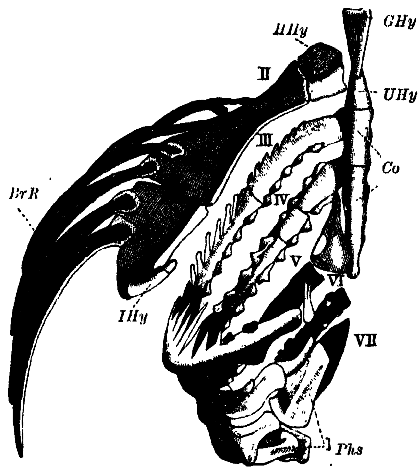


FIG. 26.

Right half of the hyoid and branchial arches of the Perch (*Perca fluviatilis* Linn.). *BrR*, branchiostegal rays; *CHy*, ceratohyal; *Co*, copulae of branchial arches; *EHy*, epihyal; *GHy*, glossohyal; *HHy*, hypohyal; *IHy*, interhyal; *Phs*, upper pharyngeal bones; *UHy*, urohyal; II, hyoid arch; III-VII, branchial arches (after Cuvier).

Several opercular bones arising from a fold of skin attain a remarkably great development in both the *Ganoidei* and *Teleostei*. The foremost, or *preoperculum*, is usually a rather long, slender, slightly arched, bony plate, which is connected above with the hyomandibular, below with the quadrate. Behind this there is an *operculum*, usually of relatively large size, bounded below by a *suboperculum*, often also by an *interoperculum*, which is connected with the hinder end of the mandible.

A variable number of small dermal bones or suborbitals (*suborbitalia*) form the arched posterior and inferior margin of the orbit. The supraorbital (*SOr*) above and the lachrymal (*L*) in front are small dermal bones, which are in close connection with the cranium, but are only rarely developed.

The gill apparatus (Fig. 26) of the *Ganoidei* and *Teleostei* does not differ essentially from that of the *Elasmobranchii*, except that the gill rays supported by the hyomandibular in the latter are replaced here by opercular plates, while behind the hyoid there are never more than five (rarely four) bony arches, and the branchiostegal rays of the hyoid arch become robust bony pieces or plates. The hyoid is subdivided into an upper *epihyal*, a middle *ceratohyal*, and a small *hypohyal* (*basihyal*) consisting of two pieces; the median connecting piece (*copula*) is extended more or less forwards into the tongue as a *glossohyal*, and is sometimes covered with teeth, sometimes toothless; a second segment of bone belonging to the copula, directed backwards, is named *urohyal*. The gill arches (*branchialia*) also consist each of three pieces (*epi-*, *cerato-*, and *hypobranchiale*), connected in the median line with copulae, and beset throughout their entire length with delicate cartilaginous rays, sometimes also on their inner side with tooth-like prominences or spines. With the epibranchials are also connected the short upper *pharyngeal* bones, which often bear teeth. The last branchial arch is usually more or less modified, and forms the lower pharyngeal bones.

The limbs of fishes comprise not only the paired, but also the unpaired fins, since both function as organs of locomotion. The paired fins correspond with the extremities of the higher Vertebrata, the pectoral fins with the anterior, the pelvic or ventral fins with the posterior limbs.

Both the pectoral and pelvic fins are connected with originally cartilaginous arches (pectoral and pelvic girdles), which may become ossified and covered with bony plates in variable number. They are entirely absent only in *Amphioxus* and the *Cyclostomi.* Except in the *Elasmobranchii,* the pectoral girdle is usually fixed to the supraoccipital or pterotic bone. In the *Elasmobranchii* (Fig. 27, *A*) it forms a simple arch of cartilage, ventrally closed, situated behind the gills, its upper ends either terminating freely (sharks) or connected with the vertebral column (rays); it is bent upwards at the insertion for the fins, and pierced by nerve foramina. In many Ganoids (*Chondrostei, Crossopterygii*) the primary cartilaginous pectoral girdle, divided

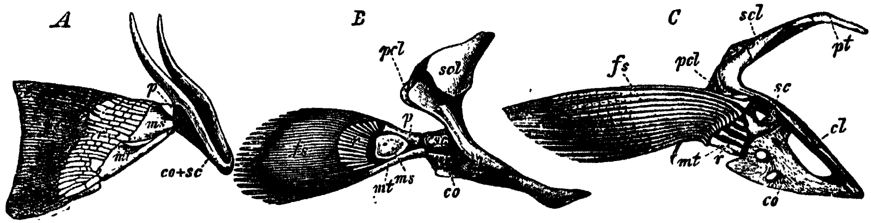


Fig. 27.

Pectoral arch and fin of *A*, *Heptanchus* (*Elasmobranchii*). *B*, *Polypterus* (*Ganoidei*). *C*. *Salmo* (*Teleostei*). *cl*, cleithrum; *co*, coracoid; *fs*, outer dermal fin rays (exoskeletal); *ms*, mesopterygium; *mt*, metapterygium; *p*, propterygium; *pcl*, postcleithrum; *pt*, post-temporal; *r*, basal rays (endoskeletal); *sc*, scapula; *scl*, supracleithrum.

into two pieces by a ventral suture, is covered on each side by three membrane bones, of which the median and largest is termed *cleithrum*, the lower one *clavicula*, the upper one *supracleithrum.* The latter is usually divided into two pieces, of which the upper is named *post-temporal.* In the other Ganoids and the Teleosteans the primary pectoral girdle is entirely replaced by ossification. The girdle is here formed of two bones united by jagged suture on the postero-internal face of the very large *cleithrum*, the hinder element homologous with the *scapula*, the antero-inferior element with the *coracoid.* In several families there is also a third, slender, arched bar (*Spangenstück*, *precoracoid*, or *mesocoracoid*), extending downwards and inwards to the lower end of the cleithrum.

The *cleithrum* is always the principal bone of the pectoral girdle in the *Teleostei*, and its size and form vary remarkably. A *supracleithrum* and a *post-temporal* (*Pt*) rest on its upper end; while an ordinarily slender accessory dermal bone, the *postcleithrum*, overlaps it behind.

The pectoral fins themselves can only be homologised in part and with difficulty with the anterior extremities of the higher Vertebrata (Fig. 30).[1]

[1] *Broom, R.*, The Origin of the Cheiropterygium. Bull. Amer. Mus. Nat. Hist., vol. xxxii., p. 459, 1913.—*Gregory, W. K.*, Origin of the Tetrapoda. Ann. New York Acad. Sci., vol. xxvi., p. 363, 1915.—*Gregory, W. K.*, *Miner, R. W.*, and *Noble, G. K.*, Carpus of *Eryops* and Structure of Primitive Chiropterygium. Bull. Amer. Mus. Nat. Hist., vol. xlviii., art. x., 1923.—*Petronievics, B.*, Pectoral fin of *Eusthenopteron.* Ann. Mag. Nat. Hist. [9], vol. ii., p. 471, 1918.—*Romer, A. S.*, Pectoral Limb Musculature and Shoulder-Girdle Structure in Fish and Tetrapods. Anatomical Record, vol. 27, p. 119, 1924.—*Romer, A. S.*, and *Byrne, F.*, The Pes of *Diadectes*: Notes on the primitive Tetrapod Limb. Palaeobiologica, vol. iv., p. 25, 1931.—*Watson, D. M.S.*, Primitive Tetrapod Limb. Anat. Anzeig., vol. xliv., p. 24, 1913.

They appear to have originated as the front part of a paired lateral fin fold, which, according to Cope, is still to be seen, though subdivided into several pairs of fins, in certain Lower Devonian *Acanthodii* (*Climatius*, p. 53). At first they must have been stiffened with parallel bars of endoskeletal cartilage, which are still shown in the Upper Devonian sharks of the Order *Pleuropterygii* (*Cladoselache*, p. 57). In these sharks the bars of cartilage are becoming modified by crowding and by some fusion at the base. One result of this crowding, and subsequent cross-jointing, seems to have been the production of an elongated fin with a median axis of cartilage which is fringed on either side with shorter cartilages, as in the Carboniferous and Permian sharks of the Order *Ichthyotomi* (*Pleuracanthus*, p. 61). A similar biserial fin occurs in the Dipnoan *Ceratodus* (Fig. 29), and in this case it was studied by Gegenbaur, who was led by comparative anatomy to suppose that it represented the most primitive type of paired fin, or *archipterygium*. In most *Elasmobranchii*, however, there is no such extreme narrowing of the endoskeletal base of the pectoral fins. There are usually three large adjacent basal cartilages, the *pro-*, *meso-*, and *metapterygium*, connected with the pectoral girdle, and each bears several rays consisting of pieces of cartilage (Fig. 28). The metapterygium is always the stoutest; the two others are often much reduced or may even be completely absent. The dermal part of the fin is itself always supported by numerous horny filaments in pairs.

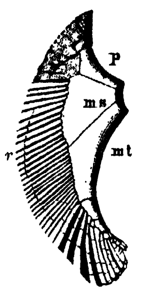


FIG. 28.

Pectoral fin of *Squatina vulgaris* Risso. With outer dermal rays removed. *ms*, mesopterygium; *mt*, metapterygium; *p*, propterygium; *r*, radials.

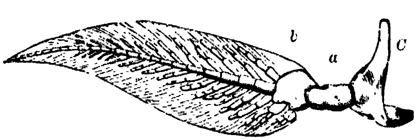


FIG. 29.

Pectoral fin of *Ceratodus forsteri* Krefft. Recent; Queensland. *a*, basal cartilage; *b*, fin; *C*, pectoral arch.

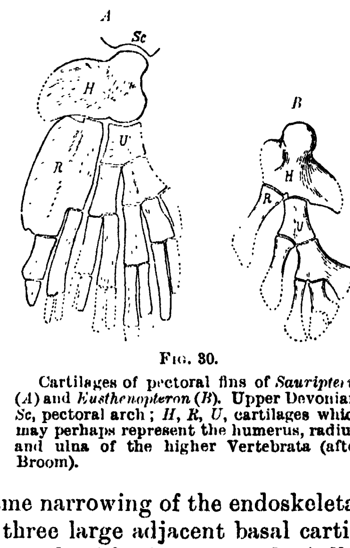


FIG. 30.

Cartilages of pectoral fins of *Sauripterus* (*A*) and *Eusthenopteron* (*B*). Upper Devonian. *Sc*, pectoral arch; *H*, *R*, *U*, cartilages which may perhaps represent the humerus, radius, and ulna of the higher Vertebrata (after Broom).

In many of the most primitive *Ganoidei* the pectoral fin is also in the form of Gegenbaur's archipterygium fringed with horny rays, and thus of the *crossopterygian* type. In most of the *Ganoidei*, however, as in the *Teleostei*, the endoskeletal basal supports are extremely degenerate, and the relatively large fin membrane is supported by bony dermal fin rays (the *actinopterygian* type).

The so-called pelvic girdle of the hinder extremity is considerably simpler than the pectoral girdle. Among the *Elasmobranchii* it appears as a paired or

unpaired rod pierced by nerve foramina, either lying in the longitudinal axis of the body or forming an arch, convex in front, concave behind. To this girdle are attached the two basal pieces (pro- and metapterygium) of the pelvic fin, which bear a single series of cartilaginous rays on their outer side. Among the Ganoids *Polypterus* alone retains two small pieces of cartilage as remnants of a pelvic girdle; in all other Ganoids, as well as in the *Teleostei*, the pelvic girdle is completely wanting, but the metapterygium of each side attains a remarkable size, and forms the whole fin support, sometimes as a simple elongated bone, sometimes as a plate forking into two pieces. In the *Ganoidei* the radials at the base of the fin skeleton are occasionally bony; in the *Teleostei*, on the other hand, they are usually cartilaginous, much reduced, sometimes indeed completely absent. The membrane of the fin itself comprises numerous articulated dermal bony rays. In the *Dipnoi* the pelvic girdle exhibits a peculiar development. It consists of an unpaired, quadrangular plate of cartilage, which is produced forwards into a long process, and supports the cartilaginous axis of the biserial fin.

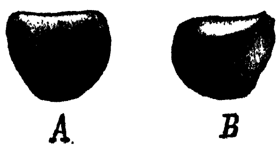


Fig. 31.
Ear bone (otolith) of a Ganoid fish (*Archaeotolithus trigonalis* Stolley), outer (*A*) and inner (*B*) aspects. Lower Jurassic; Harzburg. Nat. size (after Stolley).

While the pelvic fins of the *Elasmobranchii*, *Ganoidei*, and *Dipnoi* are always situated near the hinder end of the abdominal cavity, they are often displaced forwards in the *Teleostei*, becoming even connected with the pectoral girdle. Through this forward displacement of the pelvic fins there arise striking modifications in the general aspect of the bony fishes, which are of great importance as a means of classification.

The fossil bones of fishes can generally be recognised with certainty by their external form. Their outer surface usually exhibits a characteristic aspect, on account of numerous small rugosities, openings of canals, and striations; while tubular bones with a medullary cavity are here entirely wanting. From the histological point of view, the bones of many fishes are noteworthy for the absence or very sparse development of bone cells.

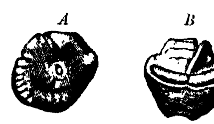


Fig. 32.
Ear bone (otolith) of a Teleostean fish, outer (*A*) and inner (*B*) aspects. Oligocene; Lattdorf. Nat. size.

Fossil ear bones or *otoliths* (Figs. 31, 32) are also sometimes found with the hard dermal structures and the skeleton. These do not consist of phosphate, but of carbonate of lime, and exhibit great variety in their shape, the sculpturing of their surface, and the nature of their borders. In those of the *Ganoidei* (Fig. 31) growth begins at one angle, while in those of the *Teleostei* (Fig. 32) it begins at the centre. Their shape is more or less constant in each group of *Teleostei*, and in many cases they can be referred to definite genera. Numerous extinct species are known only by otoliths.[1]

[1] *Bassoli, G. G.*, Otoliti fossili terziari dell' Emilia. Riv. Ital. Paleont., vol. xii., p. 36, 1906.—Otoliti fossili di pesci. Atti Soc. Nat. Modena, ser. 4, vol. xi., p. 39, 1909.—*Frost, G. A.*, Fish Otoliths from Tertiary of Atcheen, N. Sumatra. Dienst v. d. Mijnbouw Nederl.-oost-Indië, Wetensch. Meded., no. 2, 1925.—Otoliths of Fishes from the Tertiary of New Zealand and Victoria. Trans. New Zeal. Inst., vol. lix., p. 91, 1928.—Papers on otoliths of existing fishes in Ann. Mag. Nat. Hist., 1927.—*Hennig, E.*, Otolithen bei *Palaeoniscus*. Sitzb. Ges. naturf. Freunde, Berlin, 1915, p. 52.—*Koken, E.*, Über Fisch-Otolithen. Zeitschr. Deutsch. Geol. Ges., 1884, p. 500.—Neue Untersuchungen an tertiären Fisch-Otolithen, I., II. *Loc. cit.*, 1888, p. 274; 1891, p. 77.—*Malling, C.*, and *Grönvall, K. A.* [Otoliths from Lias of Bornholm.] Medd. Dansk

Finally, there are cases in which the soft parts have been preserved. Fossilised muscle[1] is not uncommon. Remains of the ovary are sometimes seen in the lower *Teleostei* (*e.g. Thrissopater* and *Osmeroides*). The structure of the kidney is clear in some specimens of the Devonian Elasmobranch, *Cladoselache*.[2] The alimentary tract is sometimes traceable by its food contents.[3]

Since the work of Aristotle, the classification of fishes has been based chiefly on the characters of the internal and external skeleton, on the nature and arrangement of the fins, and on the organs of respiration. Artedi, Bonaparte, Lacépède, Cuvier, and Valenciennes distinguished the cartilaginous fishes from those provided with a bony skeleton, and again subdivided both sections in different ways into several groups. In this classification no reference was made to fossil fishes, although sharks' teeth, for example, teeth of various bony fishes (the so-called bufonites, chelonites, toad-stones, and snakes' eyes), and also complete skeletons from different localities (*e.g.* Eisleben, Solenhofen, Oeningen, Monte Bolca, and Glarus) were already known in the eighteenth century and numbers of them had been described. The epoch-making work of L. Agassiz (1833-1844) afforded a complete survey of all the fossil fishes known at the time, and also established on scale characters a new subdivision of the fishes into four principal groups, namely, *Placoidei*, *Ganoidei*, *Cycloidei*, and *Ctenoidei*. Johannes Müller united the two latter groups under the denomination of *Teleostei* (bony fishes), defined the Ganoids more precisely, and subdivided the cartilaginous fishes into four Sub-Classes, namely, *Leptocardii*, *Cyclostomi*, *Selachii*, and *Dipnoi*. The most important of the later changes in classification consist in the establishment of the *Leptocardii* (*Amphioxus*) as an independent Class equivalent to that of the fishes, and in the closer union of the ganoids and bony fishes, which are frequently grouped under the common denomination of *Teleostomi*. The Class of fishes thus comprises the five still existing Sub-Classes of *Cyclostomi*, *Elasmobranchii*, *Dipnoi*, *Ganoidei*, and *Teleostei*; while to these must be added the extinct Sub-Classes of *Ostracodermi* (or *Ostracophori*) and *Arthrodira*, which are restricted to the Palaeozoic. No fossil remains of *Leptocardii* are known.

Geol. Foren., vol. iii., p. 295, 1909.—*Posthumus, O.*, Oligoceene en Mioceene Otolieten. Verhandl. Geol.-Mijn. Genootsch. Nederl. en Kolon., Geol. Ser., vol. vii., p. 105, 1923.—*Priem, F.*, Otolithes des poissons éocènes du bassin parisien. Bull. Soc. Géol. France [4], vol. vi., p. 265, 1906.—Otolithes des poissons fossiles des terrains tertiaires supérieurs de France. *Loc. cit.*, vol. xi., p. 45, 1911.—Otolithes éocènes de France et d'Angleterre. *Loc. cit.*, vol. xii., p. 246, 1912.—*Schubert, R. J.*, Die Fischotoliten des österr.-ungar. Tertiärs. Jahrb. Geol. Reichsanst., vol. 51, p. 301, 1902; vol. 55, p. 613, 1905; vol. 56, p. 673, 1906; vol. 65, p. 277, 1916 (Barton).—*Stolley, E.*, Über mesozoische Fischotoliten aus Norddeutschland. 3 Jahresb. Niedersächs. Geol. Vereins zu Hannover, 1910, p. 246. Also *loc. cit.*, 1912, p. 21.—*Voigt, E.*, Fischotoliten in einem Senongeschiebe. Zeitschr. f. Geschiebeforschung, vol. ii., p. 172, 1926.—*Vorstman, A. G.*, Tertiaire Vischotolieten van Java. Dienst v. d. Mijnbouw Nederl.-oost-Indië, Wetensch. Meded., no. 5, p. 1, 1927.

[1] *Reis, O. M.*, Die Petrificirung der Muskulatur. Archiv f. mikroskop. Anatomie, vol. xli., p. 492, 1893.—*Dean, B.*, The Preservation of Muscle-fibres in Sharks of the Cleveland Shale. Amer. Geologist, vol. xxx., p. 273, 1902.

[2] *Dean, B.*, Studies on Fossil Fishes. Mem. Amer. Mus. Nat. Hist., vol. ix., p. 233, 1909.

[3] *Neumayer, L.*, Vergleichend anatomische Untersuchungen über den Darmkanal fossiler Fische. Abhandl. Bay. Akad. Wiss., math.-phys. Kl., vol. xxix., p. 1, 1919.

Sub-Class 1. OSTRACODERMI.[1] (*Peltocephalata* Patten.)

Early Palaeozoic fishes with persistent notochord, and endoskeleton not usually calcified. With very primitive jaws and only pectoral paired fins; without actinotrichia in median fins. Exoskeleton well developed, the head and anterior portion of the trunk usually covered with plates, which are highly vascular in the middle layer, and always retain as a superficial layer the tubercles of dentine which are the sole covering of the more generalised forms.

The Ostracoderms form one of the most characteristic groups of the early Palaeozoic fish fauna; but their true systematic position is still uncertain. Their remains were formerly compared with the armour of reptiles such as tortoises, and also with crabs and water-beetles; while more lately they have even been supposed to exhibit resemblances to Arachnids. They were first recognised as fishes by Agassiz, and referred by him to the *Ganoidei*. A study of the internal anatomy of the *Cephalaspidae* by E. A. Stensiö confirms the opinion of E. D. Cope and A. S. Woodward that the Sub-Class is most nearly related to that of the *Cyclostomi*.

The Ostracoderms include the oldest known fish remains from the Ordovician of North America, and range through the Silurian and Devonian in both Europe and North America. The three Orders of *Anaspida*, *Heterostraci*, and *Osteostraci* are definitely recognised, and a fourth Order, *Antiarchi*, probably belongs to them. The *Anaspida* are fusiform freely swimming fishes, the others have a depressed head and trunk and must have lived on the bottom. In the *Anaspida* the dermal tubercles on the head region are not much fused, and in the more primitive of the *Heterostraci* the whole body is covered with dermal tubercles like the shagreen of sharks. In the great majority of Ostracoderms, however, the head and anterior abdominal region are covered with symmetrically arranged dermal plates. The *Heterostraci* and *Osteostraci* were united by J. V. Rohon in a Sub-Class *Protocephali*.

Order 1. ANASPIDA.[2]

Laterally compressed fusiform or elongate-fusiform fishes, with the lobe of the body in the tail turned downwards (hypocercal). Exoskeleton of the head, when complete, consisting of numerous symmetrically arranged small plates or scales, which pass gradually into the squamation of the trunk; flank scales in regular transverse series and more or less deepened. Mouth nearly terminal. Orbits laterally placed; a single median narial opening above. Gill cavity opening by an oblique row of 6 *to* 15 *perforations on each side at the back of the head.*

[1] *Gaskell, W. H.*, The Origin of Vertebrates. London, 1908.—*Kiær, J.*, Structure of the Mouth of the Oldest Known Vertebrates, Pteraspids and Cephalaspids. Palaeobiologica, vol. i., p. 117, 1928.—*Patten, W.*, The Evolution of the Vertebrates and their Kin. Philadelphia, 1912.—*Stensiö, E. A.*, The Downtonian and Devonian Vertebrates of Spitsbergen. Skrifter om Svalbard og Nordishavet, no. 12; Norsk. Vidensk. Akad. Oslo, 1927→.—*Stromer, E.*, Bemerkungen über die ältesten bekannten Wirbeltierreste. Sitzb. Bay. Akad. Wiss., math.-naturw. Abt., 1920, p. 9.—Weitere Bemerkungen. *Loc. cit.*, 1926, p. 83; 1930, p. 107.—*Woodward, A. S.*, Presidential Address, Proc. Linn. Soc., London, Sess. 132, 1920.

[2] *Bulman, O. M. B.*, General Morphology of the Anaspid, *Lasanius* Traquair. Ann. Mag. Nat. Hist. [10], vol. vi., p. 354, 1930.—*Kiær, J.*, The Downtonian Fauna of Norway. I. Anaspida. Videnskapsselsk. Skrift., Mat.-naturv. Kl., 1924, no. 6. Oslo, 1924.—*Stetson, H. C.*, *Lasanius*. Journ. Geol., vol. xxxv., p. 247, 1927.—*Birkenia*. *Loc. cit.*, vol. xxxvi., p. 458, 1928.—*Traquair, R. H.*, Fossil Fishes, Silurian S. Scotland. Trans. Roy. Soc. Edinb., vol. xxxix., no. 32, 1899; vol. xl., no. 33, 1905.—*Woodward, A. S.*, *Euphanerops*. Ann. Mag. Nat. Hist. [7], vol. v., p. 418, 1900.

All small, from 2 to 20 cm. in length. The microscopical structure of the exoskeleton is unknown.

As pointed out by Stensiö, the larva of the existing *Petromyzon* has a hypocercal tail.

Family 1. **Birkeniidae.**

Row of flank scales at dorsal and ventral borders of abdominal region inclined downwards and forwards, all others regularly inclined downwards and backwards. A dorsal median row of enlarged scutes. External ornament tubercular. A pair of pectoral spines fixed to a pair of post-branchial plates. One small anal fin. Upper Silurian.

Birkenia Traq. (Fig. 33). Dorsal scutes in abdominal region depressed, in caudal region raised to a pointed apex. *B. elegans* Traq. Downtonian;

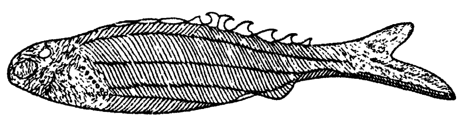


FIG. 33.
Birkenia elegans Traq. Restored outline in side view, nearly nat. size. Downtonian; Lanarkshire (after Traquair).

Lanarkshire and Ayrshire. Another species in Downtonian; Ledbury, Hereford.

? *Ctenopleuron* G. F. Matthew. Clinton Group; Westfield, New Brunswick.

Family 2. **Pterolepidae.**

A double row of flank scales at dorsal border in both abdominal and caudal regions, and one or more rows of flank scales at ventral border of abdominal region, inclined downwards and forwards; all other flank scales regularly inclined downwards and backwards. A dorsal median row of enlarged scutes, and one median enlarged scute in front of anus. A pair of pectoral spines immovably fixed to a pair of deepened post-branchial plates. An anal fin. Upper Silurian.

Pterolepis Kiær (Figs. 34, 36*a*). Scales on middle of cheek forming angulated pattern. Anal fin short, with long spine. *P. nitidus* Kiær. Downtonian; Ringerike, S. Norway.

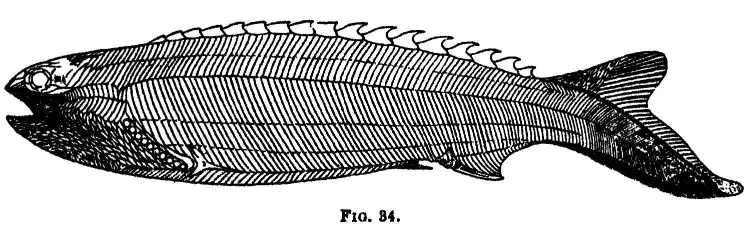


FIG. 34.
Pterolepis nitidus Kiær. Restoration, side view, nearly nat. size. Downtonian S. Norway (after Kiær).

Rhyncholepis Kiær (Fig. 36*c*). Anal fin long, with short spine. *R. parvulus* Kiær Downtonian; Ringerike.

Pharyngolepis Kiær (Figs. 35, 36*b*). Scales on middle of cheek very small

and irregular. Anal fin short, with long spine. *P. oblongus* Kiær. Downtonian; Ringerike.

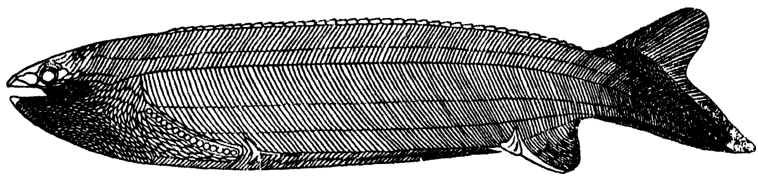


FIG. 35.
Pharyngolepis oblongus Kiær. Restoration, side view, nearly nat. size. Downtonian; S. Norway (after Kiær).

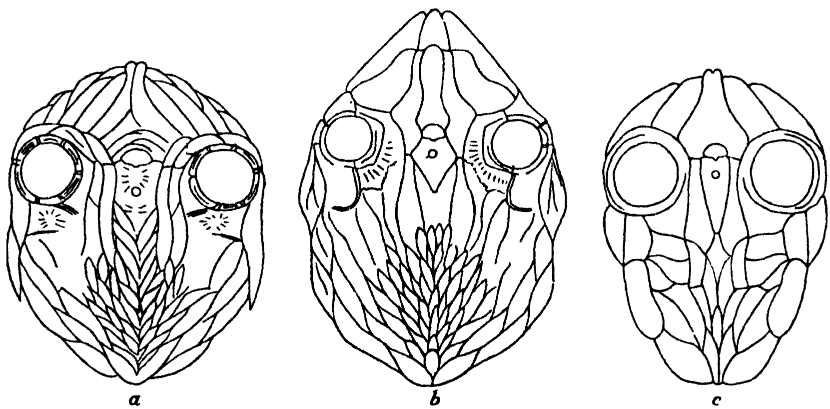


FIG. 36.
Armour of cranial roof of *Pterolepis* (*a*), *Pharyngolepis* (*b*), and *Rhyncholepis* (*c*). Downtonian; S. Norway (after Kiær). Showing orbits, pineal plate with pineal opening, and median narial opening.

Family 3. **Lasaniidae.**

Head naked. Flank squamation rudimentary or absent. A dorsal median row of enlarged scutes. Upper Silurian.

This family is referred by Stromer to a separate Sub-Order *Oligocnemata*, while the scaly families of *Anaspida* are grouped in the Sub-Order *Barycnemata*.

Lasanius Traq. (Fig. 37). Trunk naked, except immediately behind the

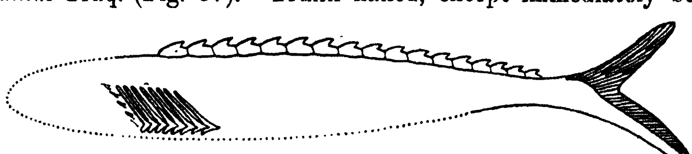


FIG. 37.
Lasanius problematicus Traq. Restored outline, nearly nat. size. Downtonian: Lanarkshire (after Traquair).

head, where a row of minute triangular scutes fringe the branchial openings, and these are followed by about eight pairs of postcephalic rods of uncertain nature. Dorsal scutes all spinous. *L. problematicus* Traq. Downtonian; Lanarkshire and Ayrshire.

Family 4. **Euphaneropsidae.**

Head covered with small tubercles, but eyes defined by hard rims. Flank scales regularly inclined downwards and backwards. A small anal fin. Upper Devonian.

Euphanerops A. S. Woodw. *E. longaevus* Woodw., the type species, about 10 cm. in length, displays traces of the axial skeleton of the trunk. Upper Devonian; Scaumenac Bay, P.Q., Canada.

Order 2. HETEROSTRACI. (*Aspidorhini* Rohon.)

Head and trunk relatively large and depressed. Exoskeleton consisting of shagreen, plates, or scales, without bone cells; each fully formed plate comprising three superimposed layers—an inner "nacreous" layer usually of lamellae, a relatively thick middle zone with numerous vacuities, and an outer hard layer of dentine. Dorsal shield, when present, of few pieces, and orbits wide apart, laterally placed. Narial opening (or openings) ventrally placed. A single pair of gill openings.

Family 1. **Coelolepidae.**[1]

Head and trunk completely covered with placoid scales or tubercles of dentine scarcely if at all fused into groups; the small, slender caudal region sharply constricted from the head region and distinctly heterocercal (perhaps hypocercal). Upper Silurian and Lower Devonian, also American Ordovician.

The dermal tubercles of genera of this family have long been known from the Upper Silurian of England and the Isle of Oesel in the Baltic Sea; but until the discovery of complete fishes in the Upper Silurian of Lanarkshire, they were commonly supposed to belong to sharks. The latter discovery is considered by Traquair to indicate some close relationship between the Ostracoderms and the primitive *Elasmobranchii.*

FIG. 38.

Thelodus parvidens Ag. Dermal tubercles, nat. size (above) and enlarged, showing the base with an opening into the pulp cavity. Upper Silurian (Ludlow Bone-bed); Ludlow.

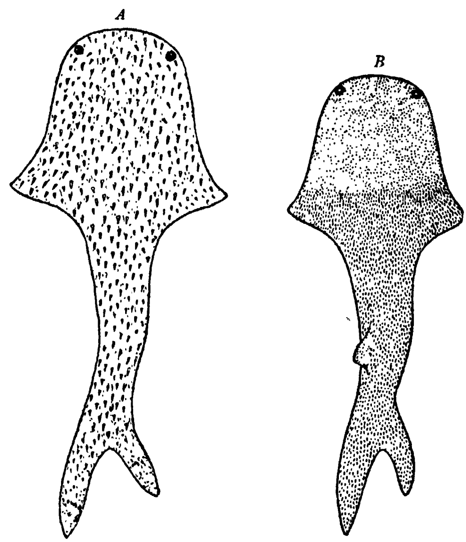


FIG. 39.

A, Lanarkia spinosa Traquair. *B, Thelodus scoticus* Traquair. Downtonian; Lanarkshire (after Traquair). About half nat. size.

[1] *Hoppe, K. H.*, Coelolepiden, etc., Insel. Oesel. Palaeontogr., vol. lxxvi., p. 35, 1931.—*Rohon, J. V.*, Die obersilurischen Fische von Oesel. II. Mém. Acad. Imp. Sci. St.-Pétersb., ser. 7, vol. xli., no. 5, 1893.—*Stetson, H. C.*, New American *Thelodus.* Amer. Journ. Sci., vol. xvi., p. 221, 1928.—Morphology of the Heterostraci. Journ. Geol., vol. xxxix., p. 141, 1931.—*Traquair, R. H.*, Fossil Fishes, Silurian S. Scotland. Trans. Roy. Soc. Edinb., vol. xxxix., no. 32, 1899; vol. xl., no. 33, 1905.—*Thelodus pagei, loc. cit.* vol. xxxix., no. 21, 1899.

Thelodus Ag. (*Coelolepis, Pachylepis, Thelolepis, Nostolepis* Pander; *Cephalopterus* Powrie; *Turinia* Traq.) (Figs. 38, 39*B*). Dermal tubercles small, quadrangular, oval, or round, and nearly uniform; the flattened outer portion slightly constricted from the large base, which is often pierced on the inner face by an opening into the pulp cavity. A small dorsal (? anal) fin near base of heterocercal (? hypocercal) tail. No enlarged ridge scales. *T. parvidens* Ag.; detached tubercles in Ludlow Bone-bed and Oesel Limestone. *T. scoticus* Traq.; complete skeletons, some showing the eyes as dark stains, in Upper Ludlow and Downtonian, Lanarkshire and Ayrshire. *T. pagei* Powrie sp.; complete skeleton, about 30 cm. in length, showing eight paired impressions probably of gill arches, from Lower Old Red Sandstone, Turin Hill, Forfarshire. *T. macintoshi* Stetson, from Upper Silurian, Nerepis, New Brunswick. ? *T. tulensis* Rohon, Upper Devonian, Malewka, Toula, Russia. An undetermined species in the Ordovician of Cañon City, Colorado, U.S.A.; also in the Lower Old Red Sandstone, Ledbury, Hereford.

Lanarkia Traq. (Fig. 39 *A*). Dermal tubercles are small, pointed, hollow spines, not of uniform size. *L. spinosa* Traq., and other species represented by skeletons in the Upper Silurian (Downtonian) of Lanarkshire and Ayrshire.

Family 2. **Pteraspidae.**[1]

Head with large rostrum, probably supported by ethmoid cartilage. Dermal armour of head and trunk completely fused into large symmetrically arranged plates. Ventral shield simple. External layer of each dermal plate forming an ornament of very fine, concentric, closely arranged ridges, usually parallel with the outer margin, rarely subdivided into tubercles; middle layer with large polygonal cancellae. Dermal sense organs well developed, arranged in canals traversing the middle layer of the shield and opening by a double series of pores externally. Tail presumably heterocercal, and scales of caudal region, when preserved, numerous and rhomboidal. Upper Silurian and Lower Devonian.

The genera of this family are distinguished according to the complexity of the dorsal shield. The simple ventral shield, similar in each form, was originally mistaken for dorsal armour, and named *Scaphaspis* by Lankester.

Pteraspis Kner (*Palaeoteuthis, Archaeoteuthis* F. Roemer; *Rhinopteraspis* Jaekel) (Figs. 40-42). Dorsal shield arrowhead-shaped, consisting of nine separately calcified plates—a large central disc; a triangular rostral plate in front; a median spine behind; a pair of orbital plates, completely enclosing the orbit on either side, and partially inserted between the rostrum and

[1] *Alth, A. von*, Über *Pteraspis, Cyathaspis,* und *Scaphaspis.* Beitr. Paläont. Österr.-Ungarns, vol. ii., 1886.—*Bryant, W. L.*, Structure of *Palaeaspis.* Proc. Amer. Phil. Soc., vol. lxv., p. 256, 1926.—*Drevermann, F.*, Über *Pteraspis dunensis.* Zeitschr. Deutsch. Geol. Ges., vol. lvi., p. 275, 1904.—*Huxley, T. H.*, On *Cephalaspis* and *Pteraspis.* Quart. Journ. Geol. Soc., vols. xii., xiv., xvii., 1856, 1858, 1861.—*Kiær, J.*, *Ctenaspis.* Skrifter om Svalbard og Ishavet, no. 33, 1930.—*Kner, R.*, Über *Cephalaspis lloydii* und *lewisii.* Haidinger's Naturw. Abhandl., vol. i., 1847.—*Kunth, A.*, Über *Pteraspis.* Zeitschr. Deutsch. Geol. Ges., vol. xxiv., 1872.—*Lankester, E. Ray*, and *Powrie, J.*, A Monograph of the Fishes of the Old Red Sandstone. I. Cephalaspidae. Mon. Palaeont. Soc., 1868.—*Leriche, M.*, *Pteraspis* de Liévin. Ann. Soc. Géol. Nord, vol. xxxii., p. 161, 1903.—Les *Pteraspis* du Dévonien de la Belgique. Bull. Soc. Belge Géol., etc., vol. xxxiii., p. 143, 1923.—*Pteraspis dunensis.* Bull. Soc. Belge Géol., etc., vol. xxxiv., p. 75 1924; vol. xxxv., p. 19, 1925.—*Lindström, G.*, *Cyathaspis* from Gotland. K. Svensk. Vet.-Akad,. Handl. Bihang, vol. xxi., sect. 4, no. 3, 1895.—*Roemer, Ferd.*, Über *Palaeoteuthis dunensis.* Palaeontogr., vol. iv., p. 72, 1855.—*Stensiö, E. A.*, Sensory Canals of *Pteraspis* and *Palaeaspis.* Arkiv f. Zoologi, vol. 18A, no. 19, 1926.—*Traquair, R. H.*, Fossil Fishes, Silurian S. Scotland. Trans. Roy. Soc. Edinb., vol. xxxix., no. 32 1899.

central disc; a pair of lateral branchial plates, each pierced by a large branchial foramen; and a pair of cornua. In one species Kiær has found a pair of small

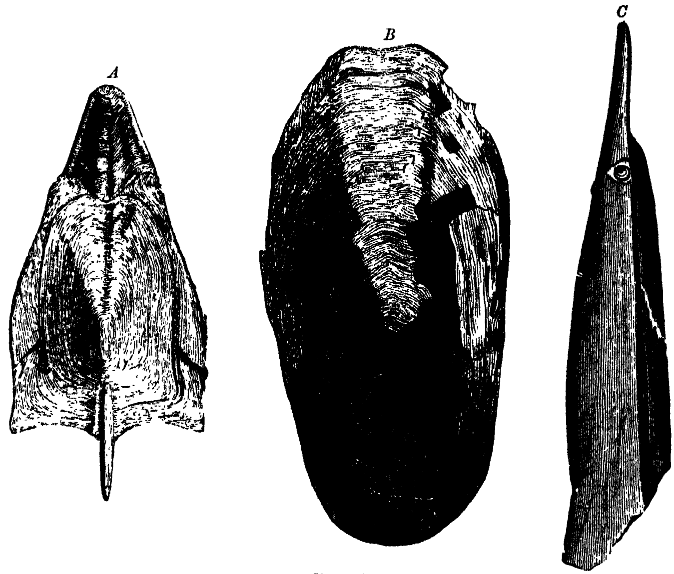


FIG. 40.

A, *B*, *Pteraspis rostrata* Ag. sp. Lower Old Red Sandstone (Cornstones); Herefordshire. *A*, dorsal shield, $1/2$ nat. size, restored. *B*, ventral shield (*Scaphaspis lloydi* Ag. sp.), $2/3$ nat. size (after Ray Lankester). *C*, dorsal and ventral shields of *Pteraspis*, lateral aspect, restored from a specimen found in Galicia (after Alth).

lateral plates bounding the sides of the anterior end of the ventral plate. A pineal pit occurs on the inner face of the shield between the orbits. A row of small antero-posteriorly elongated oral plates bounds the lower jaw,

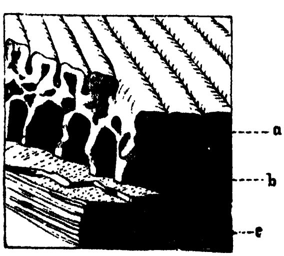


FIG. 41.

Pteraspis rostrata Ag. sp. Piece of shield, much magnified. *a*, upper, *b*, middle, and *c*, lower layer (after Ray Lankester).

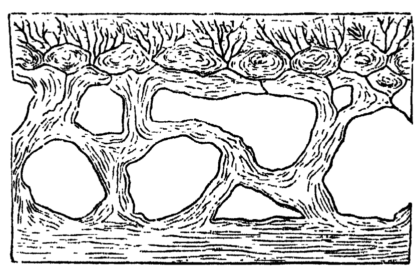


FIG. 42.

Pteraspis rostrata Ag. sp. Vertical section of head shield parallel with a longitudinal rib, highly magnified (after Ray Lankester).

and on the inner side of the oral end of each is fixed a toothplate which bears a cluster of minute pointed teeth. The upper jaw is bounded by a single plate, which bears clusters of minute pointed teeth opposed to those of the lower jaw. *P. rostrata* Ag. sp. (Fig. 40), from the Lower Old Red Sandstone of England. *P. cornubica* M'Coy sp., fragments from Lower Devonian of Cornwall. *P.* (*Rhinopteraspis*) *dunensis* Roemer sp., from the Lower Devonian

of Rhenish Prussia, Westphalia, and Belgium. Other species from Scotland, N. France, Belgium, Rhenish Prussia, Galicia, and Nova Scotia; also from the Upper Silurian of Galicia, and from the Downtonian and Lower Devonian of Spitzbergen.

Palaeaspis Claypole (*Holaspis* Lank. *nec* Gray; *Poraspis* Kiær). Dorsal shield apparently simple, without posterior spine; orbits merely forming notches. *P. americana* Clay., from Upper Silurian (Onondaga Group), Pennsylvania. *P.* (*Poraspis*) *sericea* Lank. sp., from Lower Old Red Sandstone, Monmouthshire. Other species from Downtonian, Spitzbergen.

Cyathaspis Lank. (*Diplaspis* G. F. Matthew; *Archegonaspis*, *Anglaspis* Jaekel) (Fig. 43). Dorsal shield consisting of a large central disc; two long and slender lateral cornua, which are notched anteriorly by the orbits and pierced further back by the supposed branchial foramen; and a short and broad rostral plate. Inner surface of shield showing impressions of the pineal gland, two semicircular canals of ear, and branchial chambers. *C. banksi* Huxley and Salter sp., from Upper Silurian (Ludlow Bone-bed and Downtonian) of Herefordshire. *C. schmidti* Geinitz, from Wenlock Limestone of Isle of Gotland. Other species from corresponding formations in Germany (Fig. 43), Galicia, New York, and New Brunswick, from the Lower Old Red Sandstone of England and Scotland, and from the Lower Devonian of Pas-de-Calais, France. The so-called *Scaphaspis ludensis* Salter sp., from Lower Ludlow, Leintwardine, probably belongs to this genus.

Tolypelepis Pander (*Tolypaspis* F. Schmidt). Dorsal shield as in *Palaeaspis*, but with coarse ridge ornament segregating into numerous little groups on the disc. *T. undulatus* Pand., from U. Silurian, Isle of Oesel, and Downtonian, Shropshire.

Ctenaspis Kiær. Dorsal shield as in *Palaeaspis*, but rostral region shorter, coarse ornament subdivided into tubercles, and lateral edges denticulated. *C. dentata* Kiær, shield 27 mm. long. Downtonian; Spitzbergen.

Cardipeltis, *Glossoidaspis* Branson and Mehl. Jefferson Formation; Utah, U.S.A.

? *Kallostrakon* Lankester. L. Old Red Sandstone; Ledbury, Herefordshire.

Family 3. **Drepanaspidae.**[1]

Head with small rostrum. Dermal armour of head and trunk more or less completely fused into large symmetrically arranged plates. External layer of each dermal plate forming a tubercular ornament or well-spaced concentric ridges. Middle layer denser than in Pteraspidae, *the open tissue not being regularly cancellated. Dermal sense organs not penetrating the tissue of the armour.* Devonian.

Drepanaspis Schlüter (Fig. 44). External ornament of tubercles. Dorsal armour of two median plates, surrounded in front and along the whole length

[1] *Gross, W.*, Die Fische des mittleren Old Red Süd-Livlands. Geol. u. Palaeont. Abhandl., n.f., vol. xviii., p. 123, 1930.—*Kiær, J.*, Upper Devonian Fish Remains from Ellesmere Land. Rep. 2nd Norwegian Arctic Exped., "Fram," 1898-1902, no. 33, 1915.—*Preobrajensky, J. A.*, *Psammosteus.* Sitzb. Naturf. Ges. Univ. Jurjew (Dorpat), vol. xix., p. 34, 1911.—*Rohon, J. V.*, Anatomie und Histologie der Psammosteiden. Sitzb. k. böhm. Ges. Wiss., math.-naturw. Cl., 1901, p. 1.—*Ružička, R.*, *Psammosteus* (*Ganosteus*) *perneri* n. sp. Věstnik Stát. geolog. ústavu Československ. Repub., vol. v., pt. 2-3, 1929.—*Traquair, R. H.*, Lower Devonian Fishes of Gemünden. Trans. Roy. Soc. Edinb., vol. xl., no. 30, 1903; vol. xli., no. 20, 1905. Also Geol. Mag., 1900, p. 153; 1902, p. 289.—*Woodward, A. S.*, *Psammosteus taylori.* Ann. Mag. Nat. Hist. [8], vol. viii., p. 649, 1911. Also Proc. Linn. Soc. Lond., 132nd Sess., p. 30, 1921.—*Phyllolepis concentrica.* Rep. Brit. Assoc., Australia, 1914, p. 122, 1915. Also Proc. Linn. Soc. Lond., 132nd Sess., p. 31, 1921. See also *Heintz, A.*, Skrifter om Svalbard, no. 42, 1932.

of the sides with smaller plates, of which one anterolateral pair is pierced by

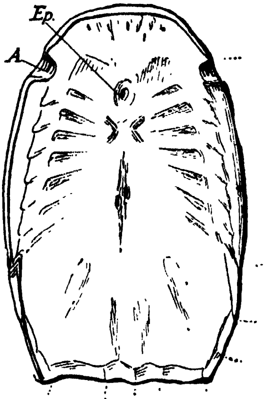


FIG. 43.

Cyathaspis (*Archegonaspis*) *integer* Kunth. Impression of inner face of dorsal shield, one-half nat. size. Upper Silurian (boulder); Erkner, near Berlin (after Jaekel). *A*, orbit; *Ep*, pineal pit, with V-shaped impressions of semicircular canals behind; paired lateral impressions of branchial chambers.

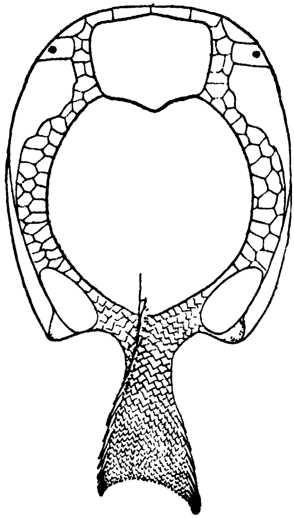


FIG. 44.

Drepanaspis gemuendenensis Schluter. Restoration of dorsal aspect, 1/3 nat. size, chiefly by Traquair. Lower Devonian; Gemünden, Hunsruck.

the orbits and two posterolateral pairs bound the branchial openings; ventral armour of a single large median plate behind, with smaller plates in front and on the sides. Tail laterally compressed, covered with rhombic scales which are deepened on the flank, and with large fulcra dorsally and ventrally; slightly hypocercal. *D. gemuendenensis* Schlüt., from Lower Devonian, Gemünden, Hunsrück, Rhenish Prussia.

Psammosteus Ag. (*Placosteus*, *Psammolepis* Ag.; *Megalaspis* Traq.). External ornament of very closely arranged, rounded or elongated tubercles which are usually crimped round the margin. One large ovoid median plate forming the greater part of the dorsal armour, a smaller ovoid median plate forming the greater part of the ventral armour, with smaller and thinner plates round the anterior and lateral borders; the lateral plates not extending so far back as the median plates and ending on each side in a solid pointed cornu directed backwards. Orbits unknown. Large ridge scutes on the tail. *P. maeandrinus* Ag., and *P. paradoxus* Ag., from Upper Devonian, Latvia. *P. taylori* Traq., from Upper Old Red Sandstone, Elgin. *P. arcticus* Kiær, from Upper Devonian, Ellesmere Land. Other

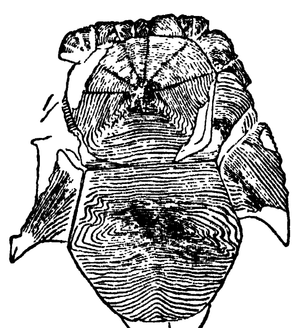


FIG. 45.

Phyllolepis concentrica Ag. Dorsal aspect, 1/3 nat. size. Upper Old Red Sandstone; Dura Den, Fifeshire (after A. S. Woodward).

species from the Lower Old Red Sandstone of west of England and Nova Scotia, from Middle Devonian of Bohemia, and from Upper Devonian, Spitzbergen.

Pycnosteus, Dyptychosteus Preobrajensky; *Ganosteus* Rohon. Upper Devonian; Latvia.

Phyllolepis Ag. (*Pentagonolepis* Lohest) (Fig. 45). External ornament of concentric ridges. Dorsal armour of two median plates, surrounded in front and along about half of each side with a series of smaller plates which ends in a pair of solid cornua pointed backwards; a single (perhaps paired) large ventral plate in hinder portion. Tail without scales, but arches of vertebral axis calcified. *P. concentrica* Ag., Upper Old Red Sandstone; Scotland. Other species in Upper Devonian of Belgium, East Greenland, Timan (N. Russia), and New York State, U.S.A. Fragments of Phyllolepid plates in Upper Devonian, Victoria and New South Wales, Australia.

Order 3. OSTEOSTRACI. (*Aspidocephali* Rohon).

Head relatively large and depressed. Dermal tubercles of head fused into small polygonal plates, with a vascular basal layer containing bone cells; these again usually fused together with an inner laminated layer containing spindle-shaped bone cells. Orbits close together; a single median dorsal narial opening. Gill cavity opening by a row of perforations on lower surface.

Family 1. **Ateleaspidae.**

Head shield rounded or tapering in front, abruptly truncated behind, consisting of loose plates. Body covered with quadrangular scales which are deepened on the flank. Tail heterocercal. Upper Silurian, perhaps also Ordovician.

Ateleaspis Traquair. Head plates finely tuberculated, scales rugose. A single dorsal fin. *A. tessellata* Traq., from the Upper Silurian (Downtonian) of Ayrshire and Lanarkshire.

Astraspis Walcott[1] may belong to a distinct family. Coarsely tuberculated plates of very open texture, without any inner laminated layer. *A. desiderata* Walcott, from Ordovician (Trenton) of Harding Quarry, near Cañon City, Colorado, U.S.A. Nearly similar plates from corresponding formations in the Bighorn Mts., Wyoming, and the Black Hills, South Dakota.

Family 2. **Cephalaspidae.**[2]

Head shield rigid, rounded or tapering in front, abruptly truncated behind, and the posterior lateral angles often produced into cornua; interorbital piece firmly fixed; an ornament of rounded or stellate tubercles. Dermal sense organs rarely leaving impressions on the exoskeleton. Body covered with quadrangular scales, which are deepened on the flank. Tail heterocercal. Upper Silurian to Upper Devonian.

[1] *Eastman, C. R.*, Proc. U.S. Nat. Mus., vol. 52, p. 237, 1917.—*Walcott, C. D.*, Bull. Geol. Soc. America, vol. iii., p. 166, 1892.

[2] *Huxley, T. H.*, On Cephalaspis and Pteraspis. Quart. Journ. Geol. Soc., vols. xii., xiv., xvii., 1856, 1858, 1861.—*Lankester, E. R.*, The Cephalaspidae. Monogr. Palaeont. Soc., 1867-69.—*Patten, W.*, Structure of Pteraspidae and Cephalaspidae. Amer. Naturalist, vol. xxxvii., p. 827, 1903.—*Rohon, J. V.*, Die obersilurischen Fische von Ösel. I. Mém. Acad. Imp. Sci. St.-Pétersb., ser. 7, vol. xxxviii., no. 13, 1892; also Bull. Acad. Imp., Mélanges géol. et paléont., vol. i., p. 223, 1896.—*Schmidt, Friedr.*, Verhandl. K. Russ. Mineral. Ges., 1873 and 1886; and Bull. Acad. Imp. Sci. St.-Pétersb., Mélanges géol. et paléont., vol. i., p. 203, 1894.—*Stensiö, E. A.*, The Downtonian and Devonian Vertebrates of Spitzbergen. Part I. Family *Cephalaspidae*. Skrifter om Svalbard og Nordishavet, no. 12; Norsk. Vidensk. Akad. Oslo, 1927.

A large collection of well-preserved head shields of *Cephalaspidae* from the

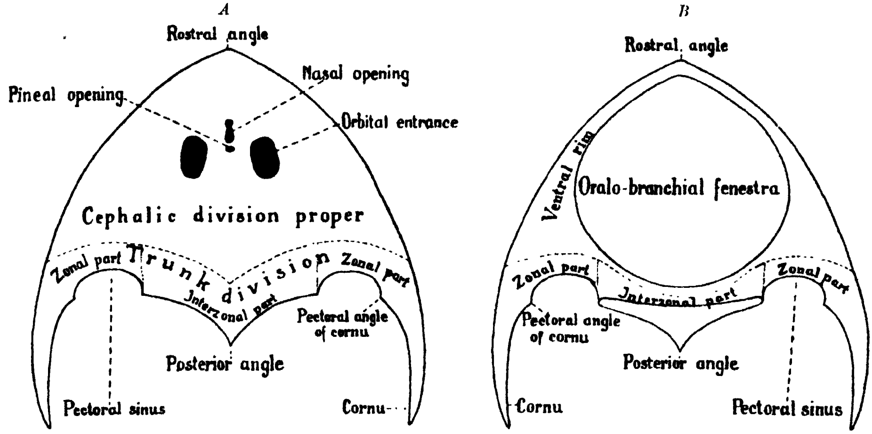


FIG. 46.

46 .Diagram of the head shield of *Cephalaspis* from above (*A*) and below (*B*), after Stensiö.

Upper Silurian (Downtonian) and Lower Devonian of Spitzbergen has been studied in great detail by E. A. Stensiö. By skilful preparation of the

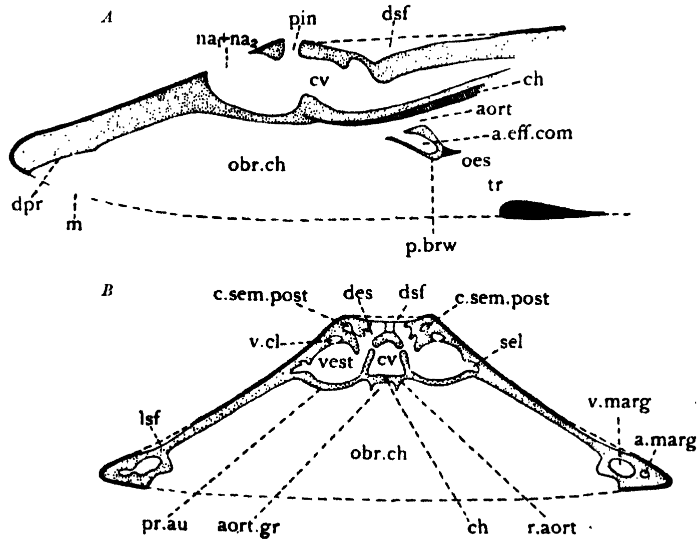


FIG. 47.

Longitudinal (*A*) and transverse (*B*) sections of the head shield of *Cephalaspis*, after Stensiö. *a. eff. com*, space for common efferent branchial artery; *a. marg*, canal for marginal artery; *aort*, aorta canal; *aort. gr*, aortal groove; *c. sem. post*, posterior semicircular canal; *ch*, notochord; *cv*, brain cavity; *dpr*, roof of mouth cavity; *des*, canal for nerve to supposed dorsal electric field; *dsf*, supposed dorsal electric field; *lsf*, supposed lateral electric field; *m*, mouth opening; na_1+na_2, narial opening and opening of hypophysial sac; *obr. ch*, gill and mouth cavity; *oes*, oesophagus; *p. brw*, post-branchial wall; *pin*, pineal foramen; *pr. au*, auditory prominence; *r. aort*, aortal ridge; *sel*, one of the nerve canals to the supposed lateral electric field; *tr*, position of the truncus arteriosus; *v. cl*, canal for the vena capitis lateralis; *v. marg*, canal for the marginal vein; *vest*, vestibular division of the labyrinth cavity.

specimens, he has been able to determine not only the arrangement of the several cavities in the skeleton of the head, but also the shape of the brain

and auditory organs and the disposition of the nerves and blood vessels (Figs. 48, 49). All the cavities and canals are lined with a perichondrial layer of bone, and the endoskeletal parts generally are more ossified in the Upper Silurian than in the Devonian species. The cartilage of the endoskeleton may have been mucocartilage like that of the larva of the existing lamprey *Petromyzon*; and, as pointed out by W. H. Gaskell, the shape of the head shield in the typical *Cephalaspis* (Fig. 46) is curiously similar to that of the mucocartilage in the head of the larva just mentioned.

As shown by vertical sections of the head shield (Fig. 47, *A*, *B*), the brain cavity (*cv*) is comparatively small immediately beneath the ridge of the roof,

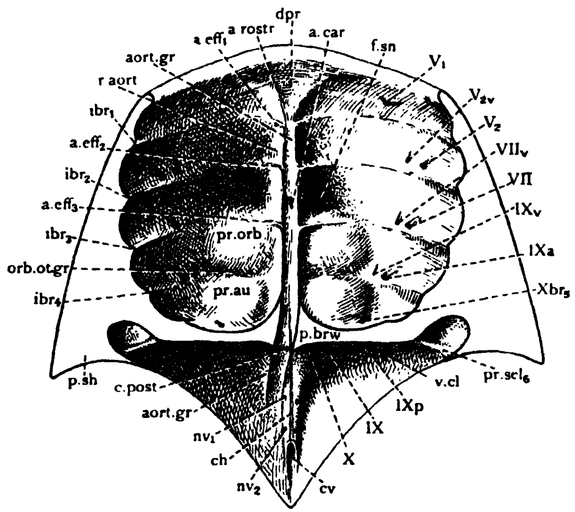


FIG. 48.

Diagram of the head shield and cranium of *Cephalaspis* from below, the unshaded area in cross-section, after Stensiö. *a.car*, pair of openings of carotid arteries; *a.eff*$_{1-3}$, grooves for efferent branchial arteries 1-3; *a.rostr*, groove for rostral artery; *aort.gr*, aortal groove; *c.post*, canal for posterior encephalic artery; *ch*, groove for notochord; *cv*, hinder end of brain cavity; *dpr*, roof of mouth cavity; *f.sn*, subnasal fossa; *ibr*$_{1-4}$, ridges between gill cavities; *nv*$_{1, 2}$, openings of spinal nerves; *orb.ot.gr*, groove between orbital and auditory prominences; *p.brw*, post-branchial wall in section; *p.sh*, endoskeletal pectoral arch in section; *pr.au*, auditory prominence; *pr.orb*, orbital prominence; *pr.sel*$_6$, ridge caused by canal occupied by the "sixth electric nerve"; *r.aort*, aortal ridge; *v.cl*, hinder opening of canal for vena capitis lateralis; *V*–*X*$_4$ openings of canals for cranial nerves.

and the cavities for the auditory organs are relatively large (*vest*). The brain must have been shaped much like that of *Petromyzon*, and the auditory organ also agrees with that of *Petromyzon* in having only two semicircular canals. The roof of the branchial chamber (Fig. 48) is marked by transverse ridges between the gills, and the shape of the cavities suggests that the gills were sac-like as in *Cyclostomi*. Large nerves (Fig. 49) spread outwards to the lateral vacuities above the branchial chambers, and also to the median post-orbital valley, and these are supposed by Stensiö to indicate the presence of electric organs in those areas. The hinder margin of the shield, with the cornua, is regarded by Stensiö (Fig. 46) as the pectoral arch, and the flexible appendages sometimes observed within the cornua are thus interpreted as pectoral fins.

Cephalaspis Ag. (*Eucephalaspis*, *Hemicyclaspis*, *Zenaspis* R. Lank.) (Figs. 50, 51). The polygonal plates of the head shield are fused into a rigid armour

except in the roof of a pair of elongated lateral chambers (presumably branchial), in the postorbital valley, in a pair of postero-lateral appendages

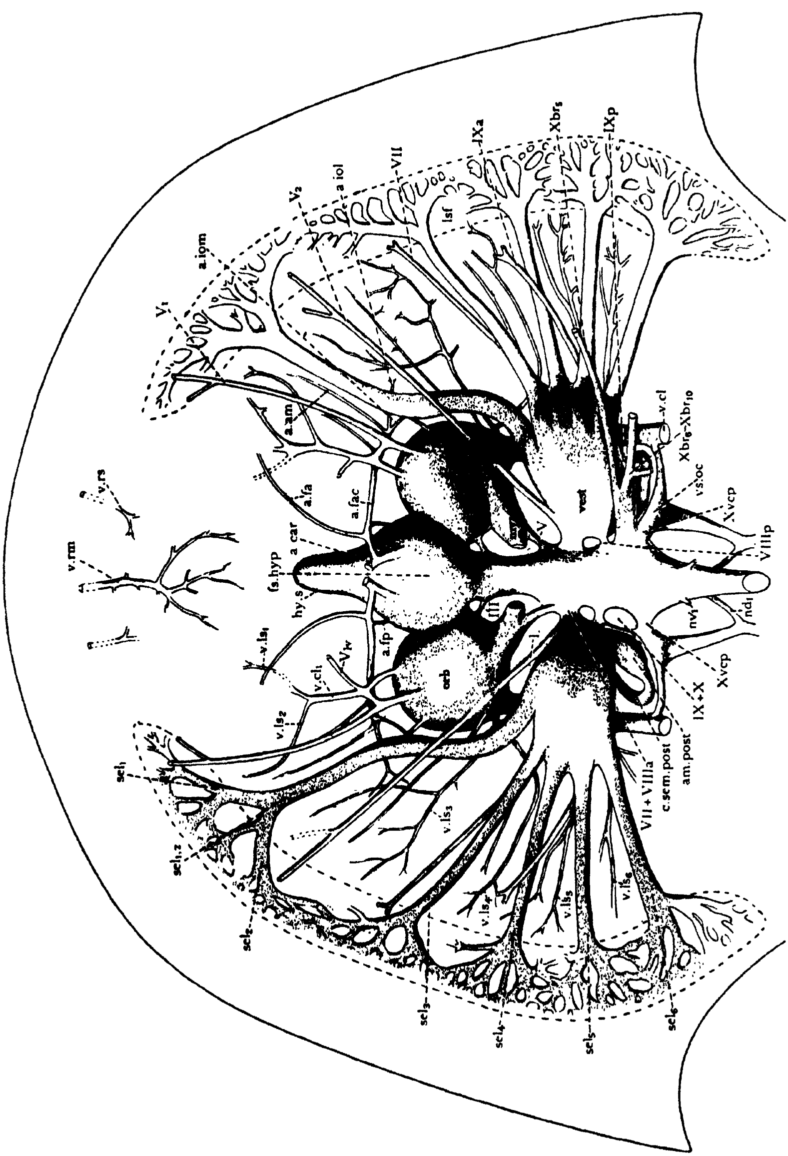


FIG. 49.

Kiæraspis auchenaspidoides Stensiö. Restored sketch of a cast of the brain cavity, orbits, auditory cavities, and certain canals, lower aspect, by Stensiö. *a.am, a.fa, a.fac, a.fp, a.iol, a.iom*, various parts of facial artery; *a.car*, carotid artery; *am.post*, posterior ampulla; $bu_{1,2}$, probably lateral buccal nerve, etc.; *c.post*, posterior encephalic artery; *c.sem.post*, posterior semi-circular canal; *fs.hyp*, fossa for hypophysis; *hy.s*, division of brain cavity for hypophysial sac; *l*, lateral fibres of trigeminus-profundus nerve complex; *lsf*, supposed lateral electric field; *my*, myodome; nd_1, nv_1, spino-occipital nerve 1, etc.; *orb*, orbit; sel_{1-6}, nerves to supposed lateral electric field; $v.cl_1$, *v.la*, etc., various veins; *vest*, vestibule of labyrinth; *vs.oc*, sinus of occipital vein; III–X, cranial nerves.

just within the cornua (Fig. 51), and on the ventral surface behind the mouth (Fig. 50). A median narial opening in front of the eyes, and a pineal pit on the inner face of the interorbital plate. A thick plate beneath the loose polygonal plates of the postorbital valley. Body triangular in transverse

section, the flanks covered with three longitudinal series of deepened scales, the middle series deepest. Ventral scales small. Cloacal opening a transverse slit far back. A single dorsal fin, triangular, at the base of the heterocercal tail; membrane of dorsal and anal fins stiffened with very small calcifications

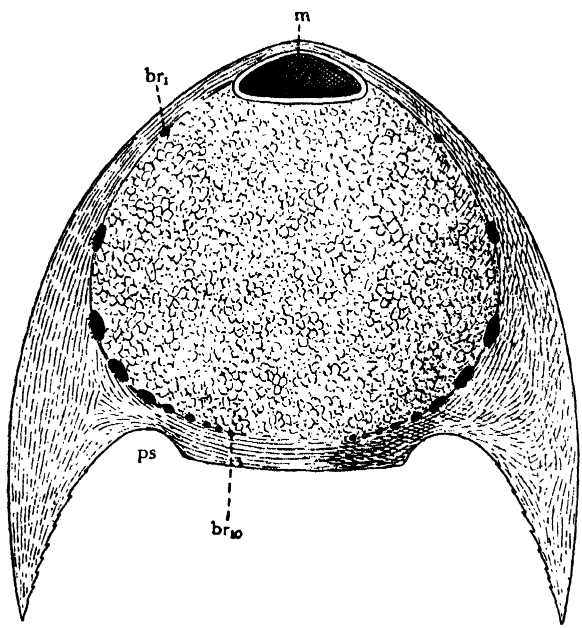


FIG. 50.
Cephalaspis sp. Diagram of ventral aspect of head shield, by Stensiö. br_{1-10}, gill openings; *m*, mouth; *ps*, pectoral sinus

which are arranged in parallel rows simulating rays. *C. lyelli* Ag. (Fig. 51), from Lower Old Red Sandstone of Scotland, west of England, and Pas-de-Calais, France. *C. magnifica* Traq., the largest known species, with shield measuring 22 cm. across, from Caithness Flagstones. Other species from

FIG. 51.
Cephalaspis lyelli Ag. Lower Old Red Sandstone; Arbroath, Scotland. 1/2 nat. size (after Ray Lankester).

Upper Silurian and Lower Devonian of Scotland, England, Norway, Spitzbergen, and Canada. One species (*C. laticeps* Traq.) from Upper Devonian, Scaumenac Bay, Canada.

Aceraspis Kiær. As *Cephalaspis*, but with two dorsal fins. Skin beneath head and front of body covered by small *Thelodus*-like scales. *A. robustus* Kiær, from Downtonian, Ringerike, S. Norway.

Micraspis Kiær. Also with two dorsal fins. Skin beneath head covered with rather large and irregular polygonal plates; a row of antero-posteriorly

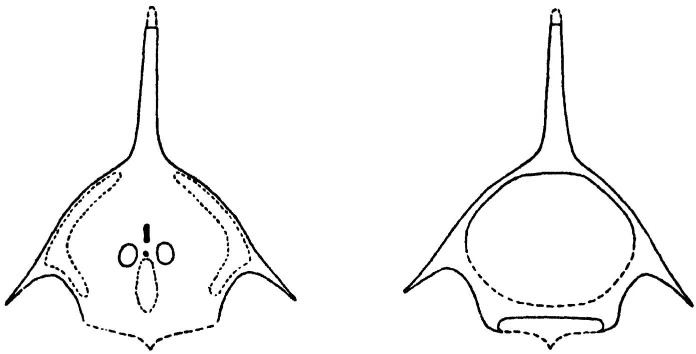


FIG. 52.

Boreaspis rostrata Stensiö. Outline of head shield, dorsal and ventral aspects, about 3 times nat. size. Lower Devonian; Spitzbergen (after Stensiö).

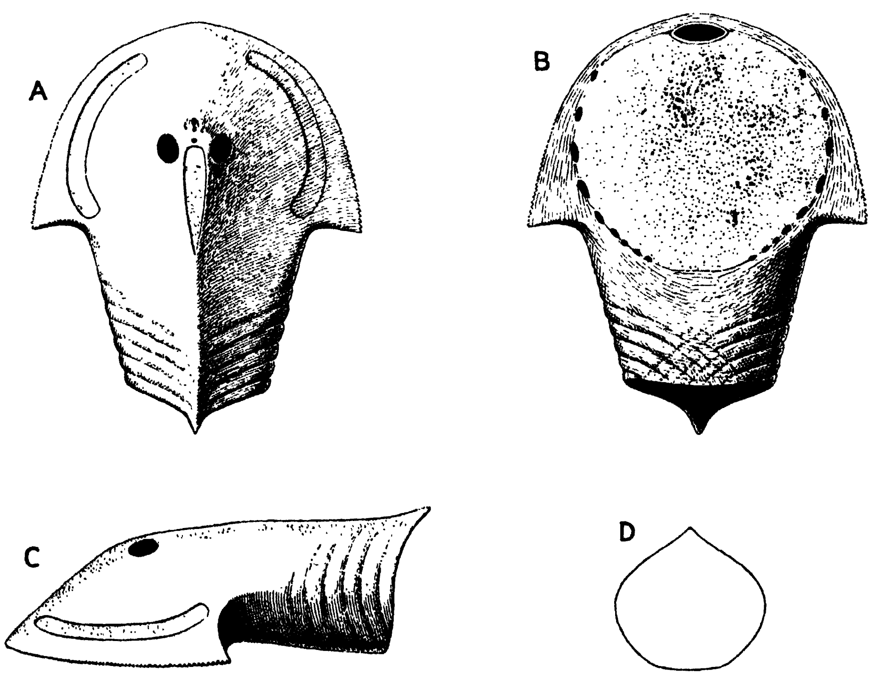


FIG. 53.

Kiæraspis auchenaspidoides Stensiö. Restoration of head shield, upper (*A*), lower (*B*), and lateral (*C*) aspects, with cross-section of trunk (*D*), about 3 times nat. size. Downtonian; Spitzbergen (after Stensiö).

elongated plates bordering lower jaw. *M. gracilis* Kiær, from Downtonian, Ringerike, S. Norway.

Benneviaspis Stensiö. Cornua directed laterally as well as posteriorly, not

extending backwards beyond hinder edge of head shield. *B. holtedahli* St., from Downtonian, Spitzbergen. *B. lankesteri* St., from Cornstones (Lower Devonian), near Malvern, England.

Hoelaspis Stensiö. Head shield short and cornua directed straight laterally. *H. angulata* St. Downtonian; Spitzbergen.

Boreaspis Stensiö (Fig. 52). Very long slender rostrum. *B. rostrata* St., with head shield only 1·5 cm. long. Lower Devonian; Spitzbergen.

Kiæraspis Stensiö (Figs. 49, 53). Head shield long and narrow, cornua small. Downtonian; Spitzbergen.

Eukeraspis Lank. Head shield as in *Cephalaspis*, but posterior cornua excessively elongated, and the flexible roof of the branchial chambers crossed by a few rigid bars. *E. pustulifera* Ag. sp., from Upper Silurian, Herefordshire.

Thyestes Eichw. (*Auchenaspis* Egerton). Head shield as in *Cephalaspis*, but three or four series of dorso-lateral scales fused into a continuous plate immediately behind it. Body depressed, ovoid in transverse section. Known species very small. *T. verrucosus* Eichw., from Upper Silurian, Isle of Oesel. So called *Auchenaspis* from Upper Silurian and Downtonian of Herefordshire. Unknown elsewhere.

Family 3. **Tremataspidae.**[1]

Head shield rounded or tapering in front, rigid, fused with the dorsal body shield, which is truncated behind; interorbital piece not fixed. A single ventral plate opposed to the dorsal body shield. Dermal sense organs forming a discontinuous groove in the armour. Upper Silurian and Lower Devonian.

Tremataspis Schmidt (Fig. 54). External surface covered with punctate ganoine, the punctations often arranged in reticulating lines; superficial

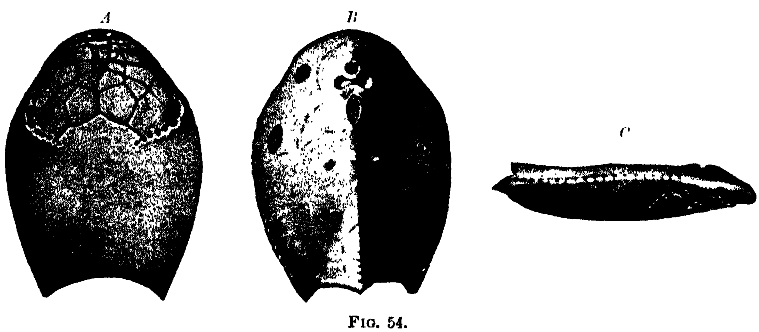


Fig. 54.

Tremataspis schmidti Rohon. Head shield, lower (*A*), upper (*B*), and lateral (*C*) aspects, nearly natural size. Upper Silurian; Isle of Oesel (after Patten).

tuberculations almost or entirely absent. Two pairs of large openings laterally placed in the anterior half of the dorsal shield seem to give flexibility to the roof of the branchial chamber. A pair of perforations apparently for the aqueductus vestibuli of the ear of each side. Ventral

[1] *Jaekel, O.*, *Trematuspis* und Pattens Ableitung der Wirbeltiere. Zeitschr. Deutsch. Geol. Ges., 1903, Protok., p. 84.—*Patten, W.*, Structure and Classification of the *Trematäspidae.* Mém. Acad. Imp. Sci. St.-Pétersb., ser. 8, vol. xiii., no. 5, 1903; also Amer. Naturalist, vol. xxxvi., p. 379, 1902.—*Wiman, C.*, Gehirn u. Sinnesorgane bei *Trematuspis.* Bull. Geol. Inst. Upsala, vol. xvi., p. 86, 1918 (criticised by *Stensiö, E. A.*, Skrifter om Svalbard, etc., no. 12, p. 303, 1927).

aspect immediately behind the position of the mouth covered with a number of symmetrically arranged polygonal plates, between which and the great ventral plate of the trunk is a transverse series of nine small branchial openings on each side. Tail covered with rhombic and polygonal scales, which have been named *Dasylepis*, *Dictyolepis*, *Melittomalepis*, and *Stigmolepis* by Pander. *T. schrenki* Pander sp., *T. schmidti* Rohon (Fig. 54), and other species in the Upper Silurian, Isle of Oesel, Baltic Sea.

Didymaspis Lankester. *D. grindrodi* Lank., from Lower Old Red Sandstone, Ledbury, Herefordshire.

Order 4. ANTIARCHI.

Dermal armour consisting of several symmetrically arranged, overlapping, large plates on the head and abdominal region. Exoskeleton with bone cells, and invested with a more or less continuous layer of ganoine. Dermal sense organs occupying open grooves on the exoskeleton. Head relatively small and articulated with the trunk. Orbits close together. A single pair of gill clefts. Apparently a pair of narial openings ventrally placed, but doubtful. A pair of paddle-like pectoral appendages, covered with dermal plates, articulated with the anterior ventro-lateral plates of the trunk. Tail heterocercal.

The bony plates of the *Antiarchi* consist of three layers with numerous bone cells, the middle layer traversed by large canals and lacunae, while the outer and inner layers exhibit a more compact texture.

Family 1. **Asterolepidae.**[1]

Exoskeleton robust and tuberculated. Dorsal and ventral shields of trunk firmly united by the lateral plates. Interorbital piece not fixed. Paddle-like appendages usually divided into a proximal and distal half by a transverse joint. One or two small dorsal fins. Middle and Upper Devonian.

Pterichthys Ag. (*Pterichthyodes* Bleeker) (Figs. 55, 56). Attaining 20 cm. in length, with the small head rounded in front, a broad and deep trunk flattened below, and a scaly tail. The upper surface of the head is covered with four pairs of lateral plates and four unpaired median plates, which are united by straight sutures. On the lower surface the cleft for the mouth is bounded in front by a pair of transversely elongated plates, which are supposed to represent the upper jaw. Behind the cleft a pair of smaller plates occurs fixed to the front of the abdominal shield. The trunk is armoured above by two large median and two pairs of lateral plates; on its ventral surface four large ventro-laterals surround a small rhombic ventro-median element. The ventro-laterals are sharply bent upwards and outwards near their lateral border to take part in covering the flank. Both the head

[1] *Gross, W.*, *Asterolepis ornata* Eichw. und das Antiarchi-Problem. Palaeontogr., vol. lxxv., p. 1, 1931.—*Hoffmann, G.*, Die Ruderorgane der Asterolepiden. Palaeontogr., vol. lvii., p. 285, 1911.—*Gerdalepis rhenanus.* Centralbl. f. Min., etc., 1916, p. 420.—*Jaekel, O.*, Organisation und Lebensweise der Asterolepiden. Palaeont. Zeitschr., vol. vii., p. 166, 1925.—*Pander, C. H.*, Die Placodermen des devonischen Systems. St. Petersburg, 1857.—*Patten, W.*, New facts concerning *Bothriolepis.* Biol. Bull., vol. vii., p. 113, 1904.—*Rohon, J. V.*, Über *Pterichthys.* Verhandl. Russ. K. Min. Ges., ser. 2, vol. xxviii., p. 308, 1891.—*Stensiö, E. A.*, Upper Devonian Vertebrates from East Greenland. Medd. om Grønland, vol. lxxxvi., no. 1, 1931.—*Traquair, R. H.*, Structure and Classification of the *Asterolepidae.* Ann. Mag. Nat. Hist., ser. 6, vol. ii., p. 485, 1888; and The *Asterolepidae.* Mon. Palaeont. Soc., 1894-1913.

plates and the dorso-lateral plates of the trunk are traversed by sensory grooves, those of the head being united by two parallel commissures. The two hinder lateral plates of the head and the adjoining body plates have bevelled edges, so that the former overlap the latter. The anterior median dorsal plate of the trunk somewhat overlaps the lateral plates, and is overlapped behind by the border both of the posterior dorso-laterals and of the posterior median dorsal plate. The orbits occur at the two ends of a transverse cleft on the upper surface of the head, and are separated by a quadrangular

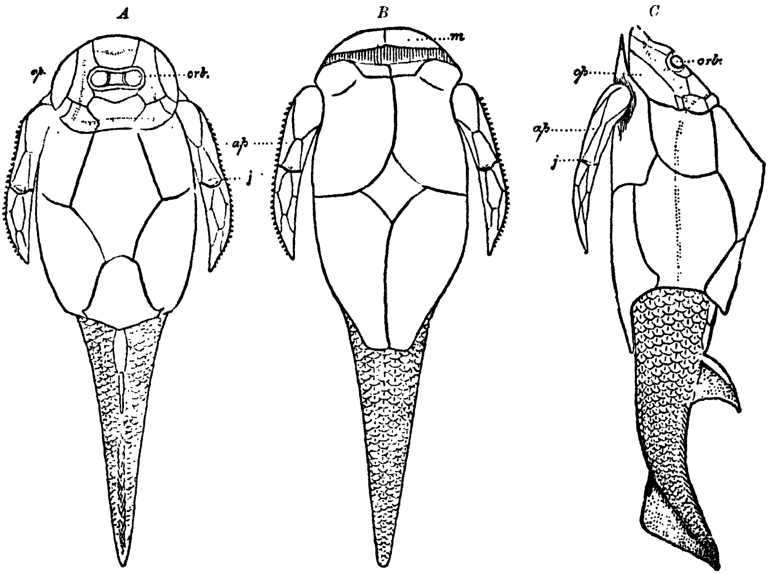


FIG. 55.

Pterichthys milleri Ag. Restoration from above (*A*), below (*B*), and in side view (*C*), 1/2 nat. size. Middle Old Red Sandstone; Scotland. *ap*, pectoral appendages; *j*, articulation; *m*, upper jaw; *op*, operculum; *orb*, orbit (after Traquair).

median plate (*os pineale*), which exhibits a small deep pit on its inner face. The two anterior ventro-lateral plates of the trunk are provided in front with an articular hollow on each side, in which are fixed the armoured paddle-shaped pectoral appendages. The latter do not reach the hinder end of the body shield, and exhibit one transverse articulation (*j*) at about their middle. The tail is covered with thin, rounded or six-sided, overlapping scales. The single dorsal fin is small. The tail is heterocercal, with large fulcral scales on its upper border, and the fin membrane confined to the lower lobe. *P. milleri* Ag. and other species represented by nearly complete examples in the M. Old Red Sandstone of Scotland. Perhaps also in Timan, N. Russia.

Asterolepis Eichw. (*Narcodes, Odontacanthus* Ag.; *Chelonichthys* Ag., in part; *Asteroplax* A. S. Woodw.). As *Pterichthys*, but often larger, and the anterior median dorsal plate overlaps both the anterior dorso-lateral and the posterior dorso-lateral plates. Chiefly represented by detached plates in the Devonian of N.-W. Russia and Latvia (*A. ornata* Eichw.) and in the Upper Old Red Sandstone of Scotland (*A. maxima* Ag.). Doubtful fragments from the Devonian of Bohemia, the Eifel, Timan (N. Russia), Spitzbergen, and Maine (U.S.A.).

Gerdalepis Hoffmann. On the visceral face of the anterior median dorsal plate, a small apical chamber is partially separated off by a pair of thin horizontal plates (see Rohon, 1891). *G. rhenanus* Beyrich, sp. Middle Devonian; Gerolstein, Eifel.

Microbrachius Traquair. *M. dicki* Traquair, from Middle Old Red Sandstone, Caithness and Orkney.

Bothriolepis Eichw. (*Pamphractus*, *Placothorax*, *Homothorax*, *Glyptosteus* Ag.) (Fig. 57). Armour nearly as in *Pterichthys*, but the pectoral appendages reaching backwards beyond the body shield, and the hinder mucus canal commissure on the head V-shaped. Plates of upper jaw notched laterally, as if for a pair of nostrils. Tail naked, with two dorsal fins and much elongated caudal fin. An Upper Devonian genus, known from N.-W. Russia, Novaia Zemlya, East Greenland, Scotland, England, Belgium, Canada, Iowa, Pennsylvania, Australia, and Antarctica. Remarkably fine examples of *B. canadensis* Whiteaves, 30 cm. in length, from Scaumenac Bay, Province of Quebec, Canada. *B. antarctica* A. S. Woodw., from Upper Devonian, Granite Harbour, Antarctica.

Fig. 56.

Pterichthys milleri Ag. Middle Old Red Sandstone; Gamrie, Scotland. *A*, Specimen in nodule, $1/2$ nat. size. *B*, Scale enlarged (after Egerton).

Remigolepis Stensiö. Appendages not jointed. U. Devonian; East Greenland and Australia; ? Colorado.

Byssacanthus Ag. A laterally compressed, longitudinally ribbed spine fixed to the ridge of a tuberculated dorsal plate. *B. crenulatus* Ag. U. Devonian; Latvia.

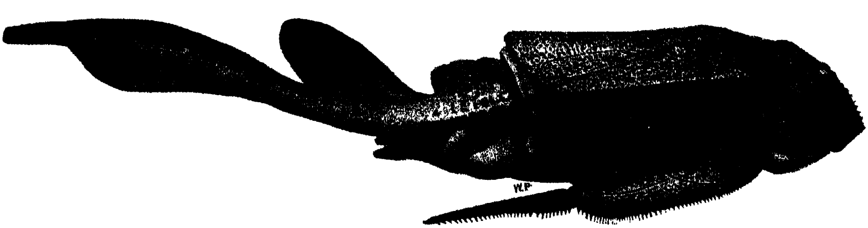


Fig. 57.

Bothriolepis canadensis Whiteaves. Side view, showing unarmoured tail with two dorsal fins and heterocercal caudal fin, $1/3$ nat. size. Upper Devonian; Scaumenac Bay, Canada (after Patten).

Cypholepis Gross. U. Devonian; Latvia.

Byssacanthoides A. S. Woodw. U. Devonian; Granite Harbour, Antarctica.

? *Ceraspis* Schlüter; *Belemnacanthus* Eastm. Middle Devonian; Eifel.

INCERTAE SEDIS.

Eoichthys Bryant.[1] An ellipsoid plate, 3 mm. in length, truncated at one end, ornamented with rows of tubercles which radiate from a point near the truncate border. Structure unknown. *E. howelli* Bryant, from Cambrian, Franklin Co., Vermont, U.S.A. Probably *Eocystis*, according to Dr. F. A. Bather.

Hunsrückia Traquair.[2] A close series of slender neural arches and spines. *H. problematica* Traq., from Lower Devonian, Gemünden, Germany.

Farnellia Traquair.[3] Calcified ring vertebrae, and polygonal dermal scutes ornamented with radiating tuberculated ridges. *F. tuberculata* Traq., about 6 cm. in length, from Lower Old Red Sandstone, Forfar. Scutes also in Ludlow Bone-bed. May perhaps belong to the *Rhenanidi* (p. 59).

Eucentrurus Traquair.[4] Elongated fish about 6 cm. in length, covered with minute spinelets, and with a pair of rows of larger double spinelets along the tapering tail. *E. paradoxus* Traq., from Lower Carboniferous (Calciferous Sandstones), Fifeshire.

Sub-Class 2. CYCLOSTOMI.

(*Marsipobranchii.*)

Vermiform fishes without ordinary jaws and without paired fins. Skull incomplete; orbits laterally placed; a single median narial opening. Notochord persistent. Skin without hard structures, and median fins supported by endoskeletal cartilages without actinotrichia; tail diphycercal or hypocercal.

The existing lampreys (*Petromyzon*, etc.) and hag fishes (*Myxine*, etc.) must be regarded as the highly specialised—in some respects degenerate—members of a very ancient group. They are, however, either unknown among fossils or represented so far only by one form, *Palaeospondylus*, which has an unusually well-calcified skeleton. Certain jaws from the Palaeozoic formations, known as Conodonts,[5] have been erroneously supposed to be teeth of this Sub-Class (see vol. i. p. 255). *Palaeospondylus* is considered to be a Dipnoan by Graham Kerr and A. E. Miller, who compare it with the skeleton of a larval *Lepidosiren*.

Palaeospondylus Traquair (Fig. 58).[6] Skull and vertebral column well calcified, not more than 5 cm. in total length. The base of the brain case is

[1] *Bryant, W. L.*, Fifteenth Biennial Report, Vermont State Geologist, p. 125, 1926.

[2] *Traquair, R. H.*, Trans. Roy. Soc. Edinb., vol. xl., no. 30, p. 736, 1903.

[3] *Traquair, R. H.*, Ann. Mag. Nat. Hist. [7], vol. ii., p. 69, 1898.

[4] *Traquair, R. H.*, Proc. Roy. Phys. Soc. Edinb., vol. xvi., p. 85, 1905.

[5] *Branson, C. C.*, Conodonts in the Permian. Science, vol. 75, p. 337, 1932.—*Holmes, G. B.*, Bibliography of the Conodonts, etc. Proc. U.S. Nat. Mus., vol. 72, art. 5, 1928.—*Ulrich, E. O.*, and *Bassler, R. S.*, A Classification of the Toothlike Fossils, Conodonts. Proc. U.S. Nat. Mus., vol. 68, art. 12, 1926.

[6] *Bulman, O. M. B.*, Note on *Palaeospondylus gunni* Traquair. Ann. Mag. Nat. Hist. [10], vol. viii., p. 179, 1931.—*Dean, B.*, The Devonian "Lamprey" *Palaeospondylus gunni*, Traquair. Mem. N.Y. Acad. Sci., vol. ii., pt. 1, 1900. Bibliography.—*Miller, A. E.*, Tail Skeleton of *Lepidosiren paradoxa*, with Remarks on the Affinities of *Palaeospondylus*. Proc. Zool. Soc., 1930, p. 783.—*Sollas, W. J.*, and *I. B. J.*, The Devonian Fish, *Palaeospondylus gunni*, Traquair. Phil. Trans. Roy. Soc., vol. 196B, no. ix., 1903.—*Traquair, R. H.*, A still further contribution to our knowledge of *Palaeospondylus*. Proc. Roy. Phys. Soc. Edinb., vol. xii., p. 312, 1894; also Proc. Zool. Soc., 1897, p. 314.

complete, with a depression for the hypophysis, but there seems to have been no cartilaginous or calcified roof or occiput. There are paired olfactory and auditory capsules, and the skull ends in front in a separate stout ring which is encircled with about eleven slender processes or cirri. The nature of the supports of the mouth is uncertain. Beneath the hinder half of the skull there are three or four pairs of rods which Sollas regards as branchial arches; from the hindmost arch a pair of large, stout, post-branchial plates extend backwards parallel with the anterior part of the vertebral column. According to Bulman, these rods and plates are better interpreted as having been connected with the base of a tongue like that of the Myxinoids, while traces of imperfectly calcified branchial arches are recognisable just behind the head. There are vertebral centra in the form of broad rings; in the abdominal region these bear short and stout neural spines, but no ribs; in the caudal region the neural and haemal spines are very slender, while the former are longer than the latter and distinctly dichotomise in their distal portions, which doubtless supported a median fin. *P. gunni* Traq., from Middle Old Red Sandstone, Caithness.

The systematic position of the so-called *Palaeomyzon* Weigelt (*ex* Jaekel MS.),[1] from the Upper Permian (Kupferschiefer) of Riechelsdorf, is uncertain.

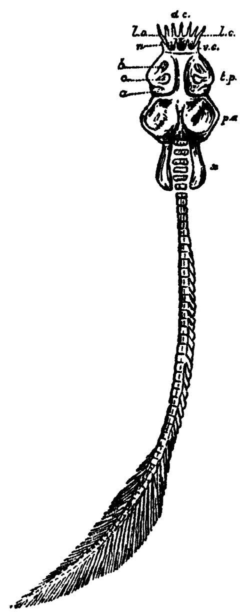


FIG. 58.

Palaeospondylus gunni Traquair. Middle Old Red Sandstone; Caithness. *a*, Separate small lobe; *b*, anterior depression or fenestra; *c*, posterior depression or fenestra; *d.c*, dorsal cirri; *l.c*, lateral cirri; *n*, supposed narial opening; *p.a*, parachordal portion of skull; *t.p*, trabeculo-palatine portion of skull; *v.c*, ventral cirri; *x*, problematical post-branchial plates. Nearly twice nat. size (after Traquair).

Sub-Class 3. ARTHRODIRA.[2]

Early Palaeozoic fishes with persistent notochord, and endoskeleton superficially calcified or ossified; no ribs. No parasphenoid bone. Head and trunk armoured with symmetrically arranged bony plates, some of which are traversed by sensory grooves; head shield movably articulated by a pair of ginglymoid joints with the body shield. Paired fins rudimentary. Supports of median fins correlated in number with the arches of the vertebral axis.

The Coccostean fishes were originally grouped by M'Coy with *Asterolepis* and *Pterichthys* in the "family *Placodermi*," and they are included by Pander in his "Placodermen." The superficial resemblance between their jaws and those of the existing *Dipnoi* was pointed out by Newberry; and they were at first provisionally regarded as an Order of *Dipnoi* by A. S. Woodward.

[1] *Weigelt, J.*, Leopoldina (Halle), vol. vi., p. 620, 1930.

[2] *Dean, B.*, Palaeontological Notes. Mem. N.Y. Acad. Sci., vol. ii., pt. 3, 1901.—Studies on Fossil Fishes. Mem. Amer. Mus. Nat. Hist., vol. ix., pt. v., 1909.—*Eastman, C. R.*, Some new points in Dinichthyid Osteology. Amer. Nat., vol. xxxii., p. 747, 1898.—Dipnoan Affinities of Arthrodires. Amer. Journ. Sci., vol. xxi., p. 131, 1906.—*Gross, W.*, Die Arthrodira Wildungens. Geol. u. Palaeont. Abhandl., n.f., vol. xix., p. 1, 1932.—*Heintz, A.*, Bau der Arthrodira. Acta Zoologica, vol. xii., p. 225, 1931.—*Hussakof, L.*, Studies on the Arthrodira. Mem. Amer. Mus. Nat. Hist., vol. ix., pt. iii., 1906.—*Koenen, A. von*, Placodermen des norddeutschen Oberdevons. Abh. K. Ges. Wiss. Göttingen, vol. xxx., 1883.—*Stensiö, E. A.*, Head of the Macropetalichthyids and other Arthrodires. Field Mus. Nat. Hist. Chicago, publ. 232, 1925.—*Woodward, A. S.*, Crossopterygian and Arthrodiran Fishes. Proc. Linn. Soc. Lond., Sess. 134, p. 30, 1922.

The latter now agrees with Stensiö in referring them to a group closely related to the ancestors of the *Elasmobranchii.*

Family 1. **Phlyctaenaspidae.**[1]

Dermal armour covered with a strongly tuberculated or ridged layer of ganoine. Head shield notched on each side for orbits. [*Jaws unknown.*] *A pair of pectoral spines immovably articulated with the anterior ventro-lateral plates.* Lower and Middle Devonian.

The following genera are arranged by Heintz in three families, *Monaspidae*, *Mediaspidae*, and *Polyaspidae*, according to the degree of fusion of the dermal plates.

Phlyctaenaspis Traquair (*Phlyctaenius* Traq.). Median occipital plate from one-third to one-half the total length of the cranial roof, with two pairs of plates between it and the pineal and rostral plates, which are fused together. Orbits small and far forwards. Pectoral spine short and straight. *P. acadica* Whiteaves sp. Lower Devonian; Campbellton, New Brunswick. *P. germanica* Traq. Lower Devonian; Gemünden, Hunsrück. Other species in the Lower Old Red Sandstone of west of England and Poland. Probably allied genus in Middle Devonian, Gippsland, Australia.

Acanthaspis Newberry. M. Devonian; New York, Ohio, and Wisconsin, U.S.A.; Spitzbergen; Eifel. *Pholidosteus* Jaekel. U. Devonian; Wildungen.

Arctolepis Eastman (*Jaekelaspis* Heintz). Rostro-pineal plate apparently larger than in *Phlyctaenaspis*. Slender arched pectoral spine shorter than the body shield; dorsal body shield very convex and sutures between constituent plates obscure. *A. decipiens* A. S. Woodw. sp., and other species. Lower Devonian; Spitzbergen.

Lunaspis Broili. Dermal plates ornamented with concentric ridges. Pectoral spine longer than the body shield, with strong curved denticles along its outer border. Slender tail covered with keeled scales. *L. heroldi* Broili, with head and body shield about 20 cm. in length. Lower Devonian; Bundenbach and Gemünden, Hunsrück, Rhenish Prussia.

Arctaspis, *Svalbardaspis*, *Plataspis*, *Elegantaspis*, *Monaspis*, *Huginaspis*, *Mediaspis* Heintz. Lower Devonian; Spitzbergen. *Polyaspis* Heintz. Middle Devonian; Spitzbergen. *Camptaspis* Branson and Mehl. Devonian; Utah, U.S.A.

Family 2. **Coccosteidae.**[2]

External tuberculated ganoine layer of dermal armour reduced and disappearing. Head shield comprising three pairs of lateral plates, one large median occipital plate, and two symmetrical pairs of plates in front of the latter, the foremost pair

[1] *Broili, F.*, Acanthaspiden aus dem rheinischen Unterdevon. Sitzb. Bay. Akad. Wiss., math.-naturw. Abt., 1929, p. 143.—Neue Beobachtungen an *Lunaspis*. *Loc. cit.*, 1930, p. 47.—*Chapman, F.*, Generic Position of "*Asterolepis ornata* var. *australis*," M'Coy. Proc. Roy. Soc. Victoria, n.s., vol. xxviii., p. 211, 1916.—*Heintz, A.*, Die Downtonischen und Devonischen Vertebraten von Spitsbergen. II, III. *Acanthaspida*. Skrifter om Svalbard og Ishavet, nos. 22, 23, 1929.—*Traquair, R. H.*, *Phlyctaenius*, a New Genus of *Coccosteidae*. Geol. Mag. [3], vol. vii., pp. 55, 144, 1890.—*Phlyctaenaspis acadica* Whiteaves. *Loc. cit.*, vol. x., p. 147, 1893.—*Woodward, A. S.*, Lower Devonian Fish-Fauna of Campbellton, New Brunswick. Geol. Mag. [3], vol. ix., p. 5, 1892.

[2] *Branson, E. B.*, *Dinichthys terrelli*. Ohio Naturalist, vol. viii., p. 363, 1908.—*Dean, B.*, Vertebral Column, Fins, and Ventral Armoring of *Dinichthys*. Trans. New York Acad. Sci., vol. xv., p. 157, 1896; vol. xvi., p. 57, 1897.—Two new Arthrodires from Cleveland Shale. Mem. New York Acad. Sci., vol. ii., p. 87, 1901.—*Eastman, C. R.*, Dinichthyid Osteology. Amer. Naturalist, vol. xxxii., p. 747, 1898.—Certain Plates in the Dinichthyids. Bull. Mus. Comp. Zool. Harvard, vol. xxxi., no. 2, 1897.—*Heintz, A.*, New Reconstruction of *Dinichthys*. Amer. Mus.

surrounding one or two small median plates. Orbits lateral, forming notches in the

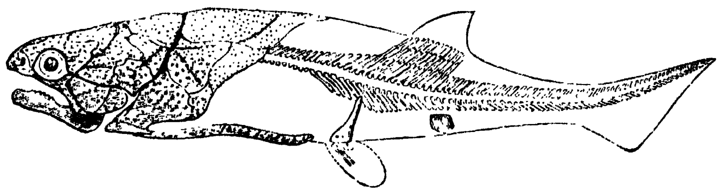


FIG. 59.

Coccosteus decipiens Ag. Restoration, $^1/_4$ nat. size. Middle Old Red Sandstone; Scotland (after A. S. Woodward). The tail may have been diphycercal, not heterocercal as shown here.

head shield; narial openings small and far forwards. Maxilla and premaxilla

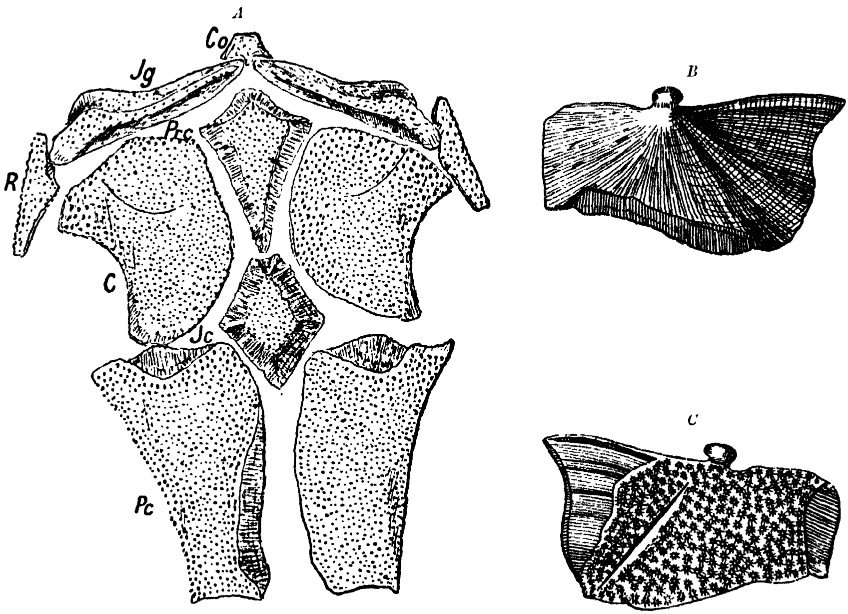


FIG. 60.

Coccosteus decipiens Ag. Plates of ventral body shield (*A*), and inner (*B*) and outer (*C*) view of left antero-dorso-lateral plate. Middle Old Red Sandstone; Scotland. *C*, anterior ventro-lateral; *Co*, median plate in front of clavicular arch; *Jc*, median ventral; *Jg*, clavicle; *Pc*, posterior ventro-lateral; *Prc*, antero-median ventral; *R*, pectoral spine. About $^1/_2$ nat. size (after Jaekel).

stouter than the pterygo-palatine arcade; usually only one ossification in each ramus

Novit., no. 457, 1931; also Dean Memorial Volume, art. iv., 1932.—Anterior-lateral Plate in *Titanichthys*. Ann. Mag. Nat. Hist. [10], vol. viii., p. 208, 1931.—*Stenognathus*. *Loc. cit.*, p. 242, 1931.—*Coccosteus*. Norsk geol. tidsskr., vol. xii., p. 291, 1931.—*Hussakof, L.*, Systematic Relationships of Certain American Arthrodires. Bull. Amer. Mus. Nat. Hist., vol. xxvi., art. xx., 1909.—Upper Devonian *Arthrodira* from Ohio in British Museum. Geol. Mag. [5], vol. viii., p. 123, 1911.—Devonic Fishes from Scaumenac Bay, Quebec (*Coccosteus*). New York State Mus., Bull. 158, p. 127, 1912.—*Jaekel, O.*, Über *Coccosteus*. Sitzb. Ges. naturf. Freunde, Berlin, 1902, p. 103.—Neue Wirbeltierfunde aus dem Devon von Wildungen. *Loc. cit.*, 1906, p. 73.—Über *Pholidosteus*. *Loc. cit.*, 1907, p. 3.—Die Mundbildung der Placodermen. *Loc. cit.*, 1919, p. 73.—*Newberry, J. S.*, Palaeozoic Fishes of North America. Mon. U.S. Geol. Surv., no. xvi., 1889 (1890).—*Obrutschew, D. W.*, *Angarichthys*. Bull. Comité Géol. Leningrad, vol. xlv., p. 679, 1927.—*Coccosteus trautscholdi*. Trav. Mus. Géol. Acad. Sci. Leningrad, vol. viii., p. 285, 1929.—*Stetson, H. C.*, Structure of *Dinichthys* and *Macropetalichthys*. Bull. Mus. Comp. Zool. Harvard, vol. lxxi., p. 19, 1930.—*Traquair, R. H.*, Structure of *Coccosteus decipiens* Ag. Ann. Mag. Nat. Hist. [6], vol. v., p. 125, 1890.

of the mandible. Teeth, when present, small and conical, but often worn away early in life. Trunk with a large median dorsal plate bearing a longitudinal median keel on its under surface; also two pairs of lateral plates, the anterior with a pair of articular processes for union with the head shield. Ventral body armour comprising two or three pairs of lateral plates and two small unpaired median plates. A pair of movable pectoral spines; a paired pelvic arch with small fins. Dorsal fin small; anal fin unknown; tail diphycercal or heterocercal. Middle and Upper Devonian.

Coccosteus Ag. (*Liognathus* Newb.) (Figs. 59, 60). Head and trunk broad, the dermal plates covered with stellate tubercles. Cranial plates united by sutures, not fused. Orbit large with a bony sclerotic ring. Besides the maxilla and premaxilla, one or two inner pairs of dentigerous bones also present in the upper jaw. Closely arranged conical teeth persistent throughout life, those of the mandibular bone not only along part of the upper edge but also along the truncated front edge. In front of the ventral body shield occur a pair of transversely elongated slender plates, probably representing the pectoral arch; a small pectoral spine, but never any traces of pectoral fins observed. Dorsal fin short-based, with a double row of supports. Tail destitute of scales. A thin median plate of bone, of uncertain nature, in vertical position beneath the vertebral column at the beginning of the tail. Nearly complete but imperfectly preserved skeletons of *C. decipiens* Ag. (Figs. 59, 60) occur in the Middle Old Red Sandstone of Scotland. *C. angustus* Traq. Lower Devonian; Gemünden, Hunsrück. Other species in Upper Devonian; England, Ireland, Germany, Russia, New York, and Canada. Also in Middle Devonian; Ohio and New York.

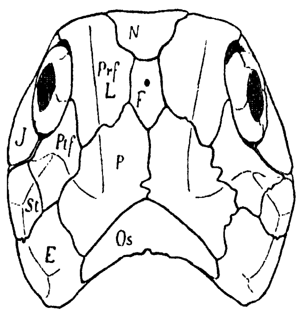


FIG. 61.

Pachyosteus bulla Jaekel. Upper view of head shield. Upper Devonian; Wildungen. *E*, lateral occipital; *F*, pineal; *J*, suborbital; *N*, rostral; *Os*, median occipital; *P*, central; *PrfL*, preorbital; *Ptf*, postorbital; *St*, marginal. 2/5 nat. size (after Jaekel).

Brachydirus v. Koenen; *Belosteus, Brachyosteus, Trematosteus* Jaekel. With vacuity in cranial roof behind pineal plate. U. Devonian; Wildungen and Bicken, Nassau.

Pachyosteus (Fig. 61), *Oxyosteus, Rhinosteus, Enseosteus, Leptosteus, Synauchenia* (*Synosteus*) Jaekel; *Hadrosteus, Leiosteus* Gross. U. Devonian; Wildungen.

Chelyophorus Ag. Upper Devonian; Govt. of Orel, Russia.

Angarichthys Obrutschew. Devonian; River Bachta, Govt. Jenissei, Siberia.

Dinichthys Newberry (*Gorgonichthys* Claypole) (Figs. 62, 63). Very large, the head sometimes measuring 1 m. in length and 0·7 m. in breadth. Tubercular ornament sparse or absent. Median occipital plate subtriangular with prominent median process behind; lateral occipital plates with very deep articular sockets for the reception of the process on the antero-dorso-lateral plates of the body shield. Median rostral and pineal plates relatively large; the pineal thickened on its inner face, with a deep conical pit but no perforation. Orbit with a ring of four large bony plates. Premaxillae and symphysial end of mandibular bones forming stout conical beaks; the trenchant margin of the maxilla and that of the mandible behind the beak in the young with small conical teeth, which are worn away, leaving only cutting edges of bone in the adult. Oral border of the pterygo-palatine arch

expanded into a punctate crushing surface. Median dorsal plate very thick, often over 0·6 m. long and broad. Antero-dorso-lateral plate overlapped by the large clavicular. *D. hertzeri* Newb. Upper Devonian (Huron Shale); Delaware, Ohio, U.S.A. *D. intermedius* Newb. (Figs. 62, 63). Cleveland Shale; Ohio. Several other species in the Middle and Upper Devonian of Iowa,

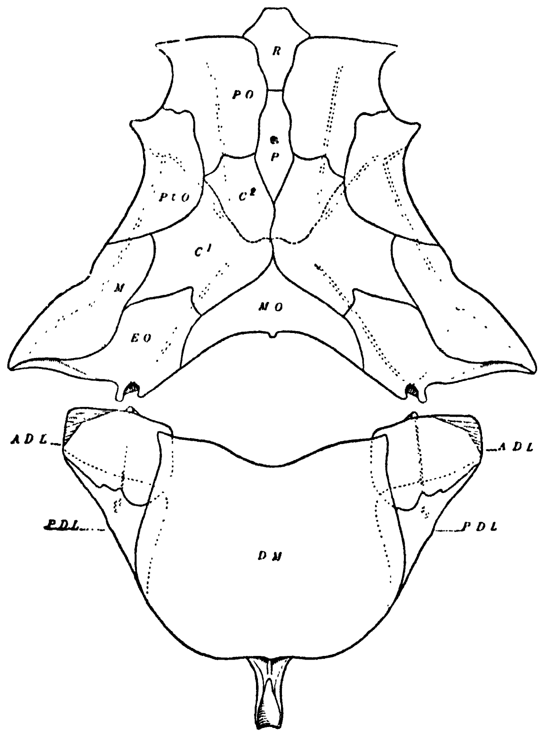


FIG. 62.

Dinichthys intermedius Newberry. Upper view of head shield and body shield. Upper Devonian (Cleveland Shale); Ohio. *ADL*, antero-dorso-lateral; *C*¹, ², central; *DM*, median dorsal; *EO*, lateral occipital; *M*, marginal; *MO*, median occipital; *P*, pineal; *PDL*, postero-dorso-lateral; *PO*, preorbital; *PtO*, postorbital; *R*, rostral. 1/6 nat. size (after C. R. Eastman).

Wisconsin, Ohio, New York, and Canada; also perhaps in the Upper Devonian of Belgium, the Eifel, Bohemia, and Russia.

Hussakofia Cossmann (*Brachygnathus* Hussakof *nec* Pomel). Upper Devonian; Ohio, U.S.A. *Grönlandaspis* Heintz. U. Devonian; E. Greenland.

Titanichthys Newberry (*Brontichthys* Claypole). Cranial shield very large, thin and flattened, much broader than long; arrangement of plates closely similar to that of *Dinichthys.* The transversely elongated ovoid pineal plate pierced by a pair of small perforations. Premaxillae, maxillae, and mandibular bones very slender and toothless, forming a small beak in front. Median dorsal plate deeply emarginate in front. Antero- and postero-dorso-laterals fused, articulated to the cranial shield by a long hinge, and overlapped by the large claviculars. *T. agassizi* N. has a horizontal expanse of 1·9 m. across head shield and claviculars. Cleveland Shale (Upper Devonian); Ohio.

Diplognathus Newberry (Fig. 64). Mandibular bone slender, pointed in front; short and stout curved conical teeth arranged in single series along

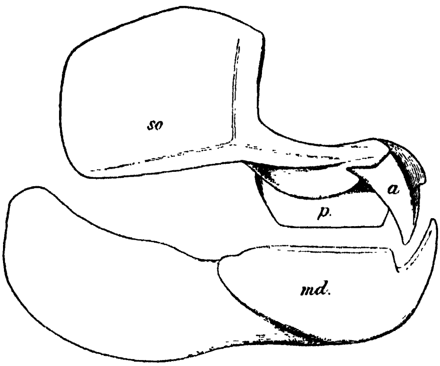


FIG. 63.

Dinichthys intermedius Newberry. Outer view of jaws, right side. Upper Devonian (Cleveland Shale); Ohio. *a*, premaxilla; *md*, mandibular plate; *p*, maxilla; *so*, suborbital. 1/4 nat. size (after A. S. Woodward).

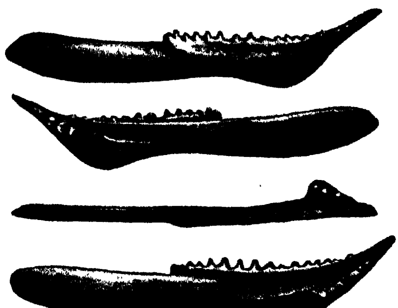


FIG. 64.

Diplognathus mirabilis Newberry. Outer, inner, and upper views of mandibular bone. Upper Devonian (Cleveland Shale); Ohio. 1/6 nat. size (after Newberry).

the oral border and the inner edge of the front border. *D. mirabilis* Newb. (Fig. 64); jaw about 30 cm. in length from Upper Devonian (Cleveland Shale), Ohio, U.S.A.

Aspidichthys, *Trachosteus*, *Glyptaspis*, *Stenognathus* Newberry. *Selenosteus*, *Stenosteus* Dean. *Protitanichthys* Eastman. Upper Devonian; Ohio, some also in New York and Michigan. *Glyptaspis eastmani* Swartz. U. Devonian; Hancock, West Virginia.

Anomalichthys von Koenen. Upper Devonian; Germany.

Holonema Newberry. Upper Devonian; North America, Shetland, and Devonshire. Middle Devonian; Belgium.

Family 3. **Homosteidae.**[1]

Head shield as in Coccosteidae, *but orbits completely within the shield, and the occipital region relatively long. Antero-lateral plates of body shield with a long anterior process which clasps the sides of the head shield.* Middle and Upper Devonian.

Homosteus Asmuss (Fig. 65). Very large fishes, broad and depressed. Jaws slender and toothless. Median occipital plate antero-posteriorly elongated; median dorsal plate of the trunk broader than long. *H. milleri* Traq. (Fig. 65), from Middle Old Red Sandstone, Caithness and Orkney. *H. formosissimus* Asmuss, from Upper Devonian of Latvia.

Heterosteus Asmuss (*Ichthyosauroides* Kutorga). Nearly resembling *Homosteus*, but larger, shorter and broader, and antero-lateral body plates with the anteriorly directed process enormous. According to Heintz, the relatively small ventral body shield is in one piece, and placed far forwards between,

[1] *Abel, O.*, Beitrag zur Kenntnis von *Heterostius convexus* Asmuss. Palaeont. Zeitschr., vol. ix. p. 314, 1927.—*Heintz, A.*, Über den Panzerbau bei *Homosteus* und *Heterosteus*. Skrift. Norsk. Vidensk.-Akad. Oslo, Mat.-Natur. Kl., 1928, no. 1.—Eine neue Rekonstruktion von *Heterostius* Asm. Sitzb. Naturf.-Ges. Univ. Tartu (Dorpat), vol. xxxvi., pt. 3, 1930.—*Traquair, R. H.*, *Homosteus* Asmuss compared with *Coccosteus* Agassiz. Geol. Mag. [3], vol. vi., p. 1, 1889.

and in contact with, the tips of the antero-lateral processes. *H. asmussi* Ag.

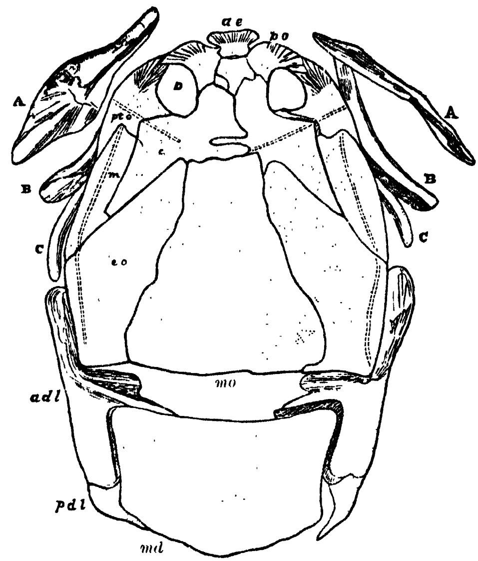


Fig. 65.

Homosteus milleri Traq. Head and dorsal shield. Middle Old Red Sandstone; Caithness. *A*, *B*, *C*, undetermined bones; *adl*, anterior dorso-lateral, with process of antero-lateral below; *ae*, rostral; *c*, central; *eo*, lateral occipital; *m*, marginal; *md*, median dorsal; *mo*, median occipital; *o*, orbit; *pdl*, posterior dorso-lateral; *po*, preorbital; *pto*, postorbital. Pineal plate behind rostral. The double lines indicate the course of the sensory grooves. 1/6 nat. size (after Traquair).

sp., common in Upper Devonian of Latvia, but known only by the massive detached plates.

Family 4. **Mylostomidae.**[1]

Dermal plates arranged as in Coccosteidae, *but smooth. Dentition for crushing, with separate dental plates in upper jaw.* Upper Devonian.

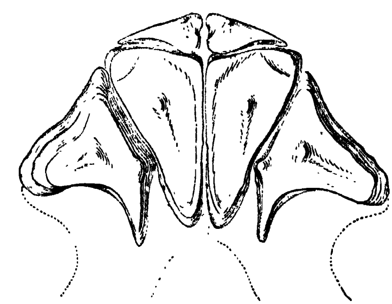


Fig. 66.

Mylostoma variabile Newberry. Dental plates, 1/4 nat. size, hypothetically arranged by Eastman. Upper Devonian (Cleveland Shale); Ohio.

Mylostoma Newberry (Fig. 66). Two pairs of upper dental plates opposed to expansion of lower jaw. *M. variabile* Newb. (Fig. 66), from Upper Devonian (Cleveland Shale), Ohio, U.S.A.

Dinomylostoma Eastman. Crushing surface of mandibular bone narrow; cartilage of lower jaw calcified. *D. beecheri* Eastm. U. Devonian; New York. Michigan.

Dinognathus Hussakof. Upper Devonian; Ohio.

[1] *Dean, B.*, *Mylostoma* Newberry. Mem. New York Acad. Sci., vol. ii., p. 101, 1901.—*Eastman, C. R.*, Structure and Relations of *Mylostoma*. Bull. Mus. Comp. Zool. Harvard, vol. l., no. 1, 1906.—Mylostomid Dentition. *Loc. cit.*, vol. l., no. 7, 1907.—Mylostomid Palatal Dental Plates. *Loc. cit.*, vol. lii., no. 14, 1909.—*Hussakof, L.*, Systematic Relationships of Certain American Arthrodires. Bull. Amer. Mus. Nat. Hist., vol. xxvi., art. xx., 1909.

Family 5. **Macropetalichthyidae.**[1]

Dermal armour covered with a strongly tuberculated layer of ganoine. Sensory canals deeply sunk in the bone. Head shield completely surrounding the orbits; median rostral and pineal plates fused; posterior articulations for body shield feeble. [Jaws and body shield unknown.] Middle and Upper Devonian.

Macropetalichthys Norwood and Owen (*Physichthys* H. von Meyer; *Agassichthys* Newberry) (Fig. 67). Head shield much arched from side to side,

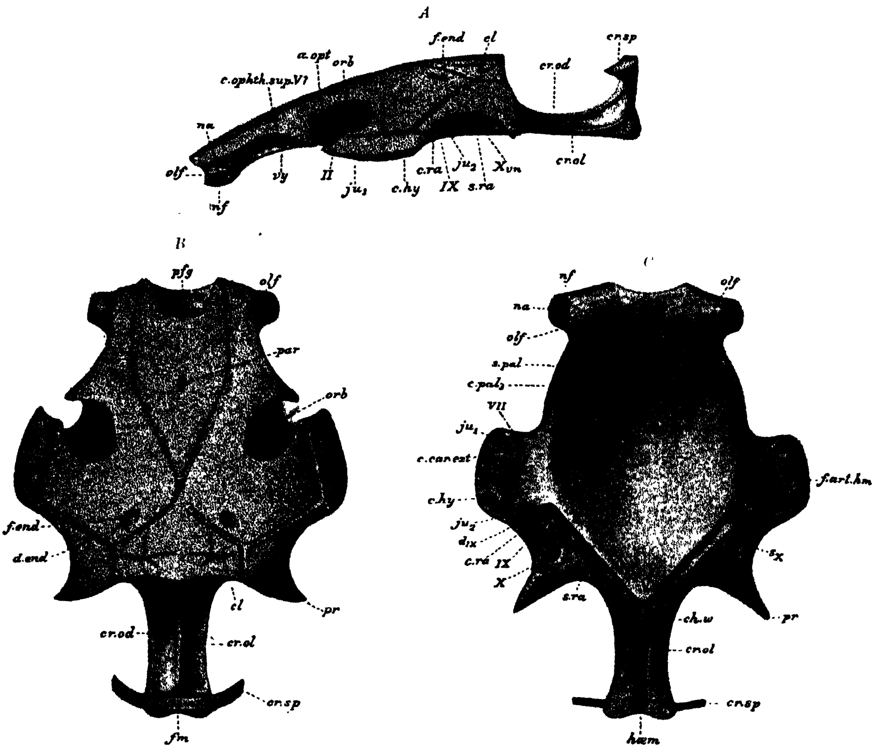


FIG. 67.

Macropetalichthys rapheidolabis Norwood and Owen. Cranium as restored by Stensiö, about 1/3 nat. size, from left side (*A*), above (*B*), and below (*C*). Middle Devonian (Corniferous Limestone); Indiana. *a.opt*, probably optic artery; *c.car.ext*, external carotid artery; *c.hy*, hyoid vein; *c.opth.sup.V?*, probably ophthalmic ramus of trigeminal nerve; *ch.w*, ridge caused by notochord; *c.pal*$_3$, palatine ramus of facial nerve; *c.ra*, radix aortae; *cl*, probably dorsal branch of vagus nerve; *cr.od*, dorsal occipital crest; *cr.ol*, lateral occipital crest; *cr.sp*, cranio-spinal process; d_{IX}, probably dorsal branch of glossopharyngeal nerve; *d.end*, ductus endolymphaticus; *f.art.hm*, probably articulation for hyomandibular; *f.end*, endolymphatic fossa; *fm*, foramen magnum; *haem*, haemal groove; *ju*, mandibular vein, etc.; *n.l*, linea lateralis nerve; *na*, narial opening; *nf*, nasal fontanelle; *olf*, nasal capsule; *orb*, orbit; *par*, pineal opening; *pfg*, anterior vacuity; *pr*, postero-lateral process of the anterior broad division of the occipital region; *s.pal*, groove for palatine ramus of facial nerve; *s.ra*, radix aortae; s_x, groove from external opening of vagus canal; *vy*, foramen; *II*, *VII*, *IX*, *X*, *vn*, nerves.

irregularly ornamented with stellate tubercles. Sensory canals large, opening by a narrow slit or a series of perforations. Occipital region relatively long; pineal plate in contact with median occipital. *M. rapheidolabis* N. and O. (Fig. 67), with head shield about 25 cm. in length, from Middle Devonian, Ohio, Indiana, and New York, U.S.A. *M. pruemiensis* Kayser, and other

[1] See reference to *Stensiö* in footnote on p. 41.

species in Middle Devonian, Eifel, Germany. *M. schei* Kiær, from Devonian, Ellesmere Land. An allied genus occurs in the Devonian of New South Wales, Australia.

Epipetalichthys Jaekel (Fig. 68). Ornamental tubercles in concentric lines.

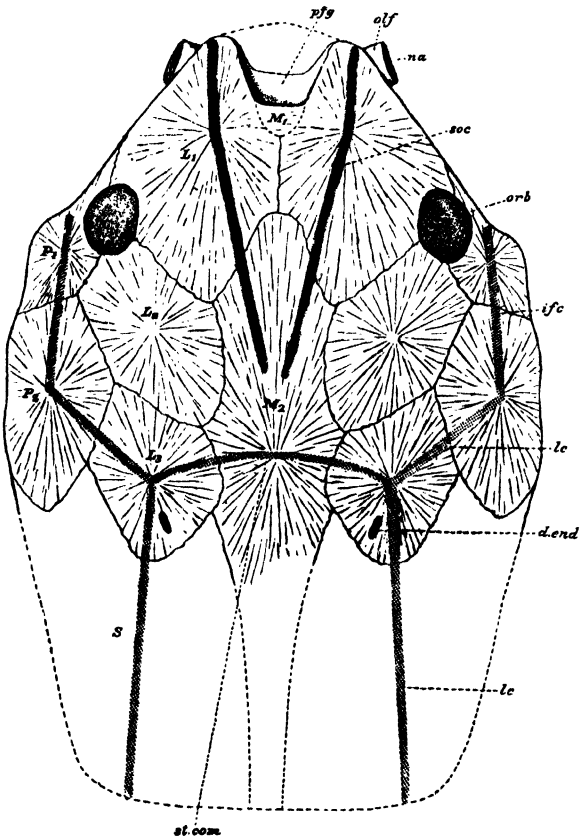


FIG. 68.

Epipetalichthys wildungensis Jaekel. Roof of skull, about $^1/_2$ nat. size. Upper Devonian; Wildungen, Germany. *L*, *M*, *P*, *S*, dermal plates; *d.end*, ductus endolymphaticus; *ifc*, infraorbital sensory canal; *lc*, main lateral line continued on head; *na*, narial opening; *olf*, nasal capsule; *orb*, orbit; *pfg*, anterior vacuity; *st.com*, supratemporal commissure of sensory canal; *soc*, supraorbital sensory canal. After Stensiö.

Pineal plate separated from median occipital. *E. wildungensis* Jaekel (Fig. 68), from Upper Devonian, Wildungen, Germany.

Family 6. **Ptyctodontidae.**[1]

Dermal armour tuberculated, much reduced. Pectoral arch covered with plates; a small movable pectoral spine. A pair of deep laterally compressed dental plates in each jaw. Middle and Upper Devonian.

[1] *Dollo, L.*, Les Ptyctodontes sont des Arthrodères. Bull. Soc. Belge Géol., vol. xxi., Mém., p. 97, 1907.—*Eastman, C. R.*, Devonian Ptyctodontidae. Amer. Nat., vol. xxxii., p. 473, 1898.—*Jaekel, O.*, Morphologie der ältesten Wirbeltiere. Sitzb. Ges. naturf. Freunde, Berlin, 1906, p. 180.—*Rohon, J. V.*, Gattung *Ptyctodus*. Verhandl. Russ.-kais. Min. Ges. St.-Petersburg [2], vol. xxxiii., p. 1, 1895.

Ptyctodus Pander (*Aulacosteus* Eichwald; *Rinodus* Newberry and Worthen). Tritoral area of dental plate composed of very hard, punctate, superimposed laminae, arranged obliquely to the functional surface. *P. obliquus* Pand., from Upper Devonian, Latvia and North Russia. *P. calceolus* N. and W. sp., from

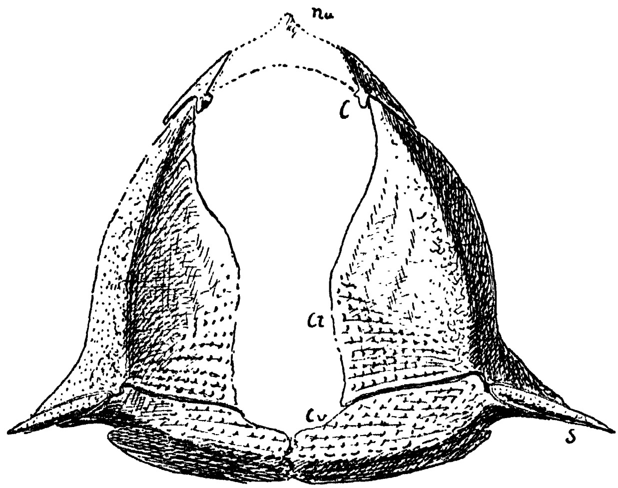


FIG. 69.

Rhynchodus major Eastman. Front view of pectoral arch, $^2/_3$ nat. size, restored by Jaekel. Upper Devonian; Wildungen. *c*, supracleithrum or anterior dorso-lateral; *ct*, cleithrum; *cv*, clavicle; *nu*, nuchal; *s*, pectoral spine.

Upper and Middle Devonian, U.S.A. Other species from Middle Devonian, Eifel, Germany, and Upper Devonian, Devonshire, Belgium, and Utah, U.S.A.

Rhynchodus Newberry (*Rhamphodus* Jaekel *nec* Davis) (Fig. 69). Dental plates with sharp cutting edges, no well-differentiated tritors. *R. secans* Newb. Middle Devonian; Ohio, U.S.A. *R. major* Eastman (Fig. 69) from Upper Devonian, Wildungen, Germany, showing dermal plates of pectoral arch. Other species from Middle Devonian, Eifel.

Rhynchodontus Jaekel. Upper Devonian; Wildungen.

Palaeomylus A. S. Woodward. Stout dental plates, with broad symphysial surface, and one punctate tritor, not laminated. *P. frangens* Newb. sp., and other species from Middle Devonian, U.S.A.

Deinodus Hussakof and Bryant. Middle Devonian; New York.

Sub-Class 4. ELASMOBRANCHII.[1]

(*Chondropterygii* Günther; *Placoidei* Ag.)

Endoskeleton cartilaginous; exoskeleton, when present, usually structurally identical with the teeth (placoid scales). Usually five (rarely six or seven) pairs of branchial arches, the clefts exposed or covered only by a flap of skin, without operculum. Paired fins well developed. Tail diphycercal, heterocercal, or gephyrocercal. In the living forms—optic nerves not decussating but forming a chiasma; bulbus arteriosus of the heart with two, three or more series of valves; air bladder absent; intestine with a spiral valve; ovaries with few large ova.

[1] *Daniel, J. F.*, The Elasmobranch Fishes. Univ. California Press, Berkeley, 1922 (also ed. 2).

The unsegmented cartilaginous cranium of the *Elasmobranchii* is more or less imperfectly hardened with polygonal granules of phosphate of lime. In the sharks and skates the pterygoquadrate cartilage of the upper jaw is movably suspended from the cranium, and the vertebral axis is often distinctly segmented; in the Chimaeroids (*Holocephali*) the upper jaw is fused with the

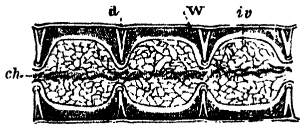


FIG. 70.

Longitudinal section of the anterior part of the vertebral column of *Heptanchus*. *ch*, notochord; *d*, incipient calcified double-cone (basis of centrum); *iv*, intervertebral space filled with notochord; w, constriction of notochordal sheath (after Kölliker).

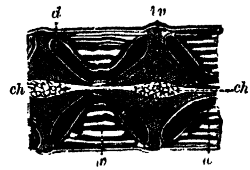


FIG. 71.

Longitudinal section of the tectospondylic vertebral column of *Squatina angelus* Linn. *ch*, notochord; *d*, calcified double-cone (basis of centrum); *iv*, intervertebral space; *w*, vertebral centra with concentric calcified rings (after Hasse).

cranium and the mandible articulates directly with this, while the notochord remains unsegmented, so that the vertebrae are always indicated only by the arches.

All the earliest Elasmobranchs and some of the Mesozoic genera have a persistent notochord, but the higher and later forms have very variously calcified vertebrae. Hasse[1] distinguished four types of vertebrae which

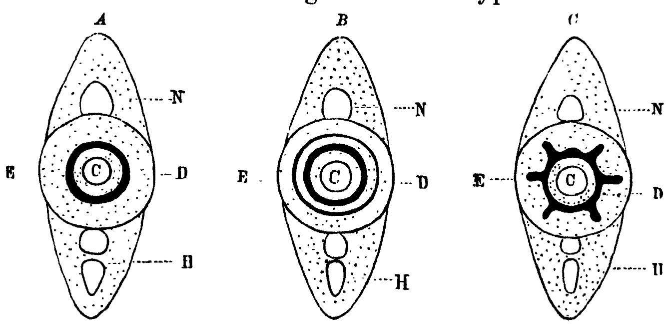


FIG. 72.

Diagrammatic vertical section through the middle of Selachian vertebrae of the *cyclospondylic* (*A*), *tectospondylic* (*B*), and *asterospondylic* (*C*) types. C, space for notochord; D, central calcified ring or double cone; E, elastica externa; H, haemal arch; N, neural arch (after Hasse).

he regarded as characteristic of four groups into which he divided the Elasmobranchs; but Ridewood[2] afterwards showed that this classification could not be maintained. Among the existing *Selachii* the *Notidanidae* exhibit the most primitive vertebral axis (Fig. 70). Here regularly spaced thickenings round the notochordal sheath constrict the chord itself and form divisions pierced through the middle (*diplospondylic*). The term *cyclospondylic* is applied by Hasse to those vertebrae in which a calcified ring appears uniting the ordinarily calcified anterior and posterior borders of the primitive constricted centrum (Fig. 72, *A*). When additional calcified lamellae concentric with the

[1] *Hasse, C.*, Das natürliche System der Elasmobranchier. Jena, 1879. Supplement in 1885.
[2] *Ridewood, W. G.*, Calcification of the Vertebral Centra in Sharks and Rays. Phil. Trans. Roy. Soc., vol. 210B, no. viii., 1921.

first are developed in the intravertebral space, the *tectospondylic* type (Figs. 71, 72, *B*) is recognised; when, on the other hand, calcified plates or ridges radiate from the centre to the periphery, the vertebrae are termed *asterospondylic* (Fig. 72, *C*).

With the vertebrae there occur most abundantly in the fossil state teeth, fin spines, and dermal tubercles and plates. Sharks' teeth are among the fossils which have been longest known, and are frequently mentioned in the older writings under the names of glossopetrae, birds' tongues, and snakes' tongues. The form of the teeth is very variable, often sharply pointed with cutting edges, single- or many-cusped, but frequently also pavement-like, with a flattened, bluntly conical crown. They consist essentially of vasodentine, dentine, and structureless enamel (ganodentine). Except in some of the extinct *Acanthodii*, they are always fixed by ligament, never fused with the supporting jaw.

The Elasmobranchs may be divided into seven Orders: *Acanthodii*, *Pleuropterygii*, *Rhenanidi*, *Stegoselachii*, *Ichthyotomi*, *Selachii*, and *Holocephali*. By O. P. Hay the Orders *Acanthodii*, *Pleuropterygii*, and *Ichthyotomi* are grouped in a Super-Order *Tapinoselachii*, and the *Selachii* in a Super-Order *Aristoselachii*.

Order 1. ACANTHODII.[1]

Endoskeleton well calcified, with dermal and membrane calcifications in the region of the skull and pectoral arch. Pterygoquadrate arcade movably articulated with the cranium (hyostylic). Orbit surrounded with a ring of four thin plates of dentine. Teeth, when present, firmly fixed to the calcified sheathing plates of the pterygoquadrate and mandibular cartilages. Notochord persistent. Endoskeletal cartilages of all the fins much reduced, and the dermal expansion almost or completely destitute of rays; each of the fins except the caudal with a robust anterior spine implanted in the flesh. Pelvic fins of male without claspers. Dermal armature of trunk consisting of small, closely arranged, quadrate granules, which also extend over the greater portion of the fins; lateral line passing between two series of the granules.

Four families of this Order are distinguished, the *Acanthodidae* with one dorsal fin, and the *Diplacanthidae*, *Ischnacanthidae*, and *Gyracanthidae* with two dorsal fins. These fishes were originally assigned to the *Ganoidei* by Agassiz, but their close relationships to the *Elasmobranchii* were observed by Lütken, Fritsch, and Huxley. While, however, they were arranged by Lütken and Fritsch among the *Elasmobranchii*, they were regarded by Huxley as intermediate between the *Ganoidei* and *Elasmobranchii*. Later researches by Traquair, A. S. Woodward, Reis, and Jaekel, seem to have justified the reference of the Order to the *Elasmobranchii*, though Goodrich has shown that the dermal covering is not typical shagreen.

[1] *Davis, J. W.*, *Acanthodidae*. Trans. Roy. Dublin Soc. [2], vol. v., no. vi., 1894.—*Dean, B.*, Notes on Acanthodean Sharks. Amer. Journ. Anat., vol. vii., p. 209, 1907.—*Fritsch, A.*, Fauna der Gaskohle in Böhmen, vol. ii. Prague, 1889.—*Huxley, T. H.*, Preliminary Essay upon the Systematic Arrangement of the Fishes of the Devonian Epoch. Mem. Geol. Surv, dec. x., 1861. —*Kner, R.*, Sitzungsb. k. Akad. Wiss. Wien, math.-naturw. Cl., vol. lvii., p. 290, 1868.—*Powrie, J.*, On the earliest known Vestiges of Vertebrate Life. Trans. Edinb. Geol. Soc., vol. i., p. 284, 1870.—*Reis, O.*, Zur Kenntniss des Skeletts der Acanthodinen. Geogn. Jahreshefte, München, 1890, p. 1, and 1894, p. 49.—Illustrationen z. Kenntnis des Skeletts von *Acanthodes bronni* Ag. Abhandl. Senckenberg. Naturf. Ges., vol. xix., p. 49, 1895.—Über *Acanthodes bronni* Ag. Morphol. Arbeiten, vol. vi., p. 143, 1896.—*Roemer, F.*, Über *Acanthodes gracilis*. Zeitschr. Deutsch. Geol. Ges., vol. ix., p. 65, 1857.—*Traquair, R. H.*, Geol. Mag., 1888, p. 511, and 1889, p. 17.

The *Acanthodii* comprise not only a number of more or less completely known genera from the Devonian, Carboniferous, and Permian formations, but probably also a few genera which are still represented only by isolated fin spines (e.g. *Haplacanthus* Ag. and *Machaeracanthus* Newberry).

Family 1. **Diplacanthidae.**

Two dorsal fins. Free spines between paired fins conspicuous. Upper Silurian to Upper Devonian.

Diplacanthus Ag. (*Rhadinacanthus* Traquair). Trunk fusiform, probably not much laterally compressed. Teeth minute or absent. Pectoral fins large, and a median pair of stout spines fixed between these to the well-developed basal supports; a single pair of free spines between the pectoral and pelvic fins. *D. striatus* Ag., about 10 cm. in length, and other species from the Middle Old Red Sandstone of Scotland. *D. horridus* A. S. Woodw. from Upper Devonian, Scaumenac Bay, Canada.

Climatius Ag. (*Brachyacanthus* Egert.) (Fig. 73). Trunk fusiform and laterally compressed. Teeth minute or absent. Fin spines remarkably

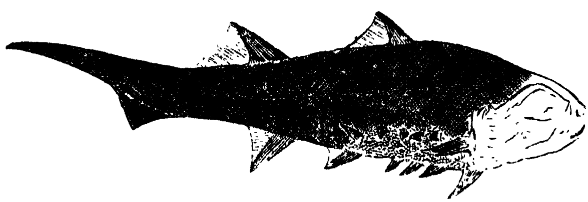


FIG. 73.
Climatius scutiger Egerton. Lower Old Red Sandstone; Forfarshire. Nat. size (after Powrie).

broad and marked with coarse longitudinal ridges, sometimes with posterior denticles; no base of insertion, but each spine fixed on an endoskeletal support. Pectoral fins not much larger than the pelvic pair; three or four pairs of free spines, resembling the fin spines, between the paired fins. *C. reticulatus* Ag. and *C. scutiger* Egert. (Fig. 73) are known by nearly complete fishes from the Lower Old Red Sandstone of Forfarshire. Similar spines occur in the Passage Beds (Downtonian) of Herefordshire, and in the Lower Devonian of Campbellton, New Brunswick.

Euthacanthus Powrie. Essentially identical with *Climatius*, but with narrower straight spines. Lower Old Red Sandstone; Forfarshire.

Parexus Ag. Much resembling *Climatius*, but the anterior dorsal spine enormously elongated and with large posterior denticles. *P. recurvus* Ag., and *P. falcatus* Powrie, from Lower Old Red Sandstone, Forfarshire.

Family 2. **Ischnacanthidae.**

Fusiform laterally compressed fishes. Two dorsal fins. No free spines between paired fins. No median pair of spines attached to pectoral arch between the pectoral fin spines. Upper Silurian and Lower (? and Middle) Devonian.

Ischnacanthus Powrie (*Ictinocephalus* Page). A few large, smooth, conical teeth alternating with minute cusps, on the edge of the jaws. A spiral or arch of conical teeth of the form named *Protodus* A. S. Woodw. at the

mandibular symphysis (see p. 56). Scales smooth. *I. gracilis* Egert. sp., from Lower Old Red Sandstone, Turin Hill, Forfarshire. Probably large species in Downtonian, England.

Plectrodus Ag.[1] Jaws from Upper Silurian; Herefordshire, Isle of Oesel (Baltic Sea), and Laundos (Portugal). *Gomphodus* Pander. Scales from Oesel.

The lower jaw with an arch of presymphysial teeth named *Onychodus sigmoides* Newberry (Fig. 74) from the Middle Devonian of Ohio and New

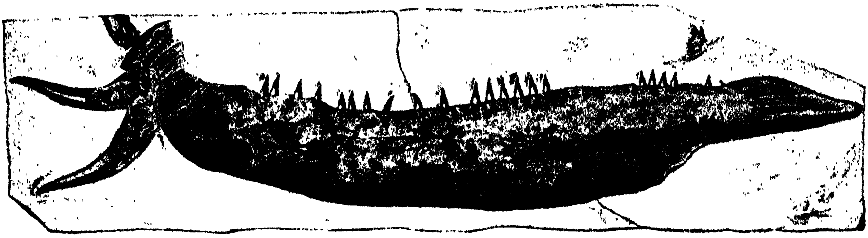


FIG. 74.

Onychodus sigmoides Newberry. Part of left ramus of lower jaw, outer view, showing remains of arch of presymphysial teeth. Middle Devonian (Corniferous Limestone); Ohio. $^1/_2$ nat. size (after Newberry).

York, U.S.A., may belong to a gigantic Acanthodian allied to *Ischnacanthus*. Scales and bones of a Crossopterygian Ganoid have been hypothetically associated with it. Similar presymphysial teeth occur in the Upper Devonian of Ohio (Fig. 75) and in the Devonian of the Eifel, Germany, and of Spitzbergen.

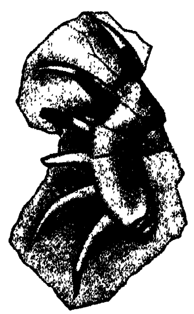


FIG. 75.

Onychodus ortoni Newberry. Arch of presymphysial teeth. Upper Devonian (Huron Shale); Ohio. $^1/_2$ nat. size (after Newberry).

Family 3. **Gyracanthidae.**

Round-bodied depressed fishes. Two dorsal fins. Pectoral fins very large, and pelvic fins advanced far forward. Lower Devonian to Carboniferous.

Gyracanthus Ag. Known only by paired fin spines (sometimes 40 cm. in length) and triangular free paired spines. Fin spines with large base of insertion, exserted portion ornamented with parallel oblique transverse ridges, which diverge in pairs from the longitudinal median line of the anterior face; often worn at apex during life. *G. formosus* Ag., from British and Irish Coal Measures. Other species throughout Carboniferous of Scotland, Ireland, and North America. *G. incurvus* Traquair, a small species from Lower Devonian, Campbellton, New Brunswick. Small species also in the Upper Devonian of New York State.

Gyracanthides M'Coy.[2] Pectoral fin spines more strongly arched and with smaller base of insertion than *Gyracanthus*, much compressed from above downwards; pelvic fin spines rounded in transverse section at the base and nearly straight, fixed completely between the hinder half of the pectorals. Two pairs of triangular free spines near base of pectorals. Tail small and slender, with small dorsal and anal fin. *G. murrayi* A. S. Woodw. known by

[1] *Woodward, A. S.*, Geol. Mag., 1917, p. 74.
[2] *Woodward, A. S.*, Mem. Nat. Mus., Melbourne, no. 1, p. 3, 1906.

nearly complete fish about 50 cm. in length, from Carboniferous, Mansfield, Victoria, Australia.

? *Cosmacanthus* Ag. Upper Old Red Sandstone; Scaat Craig, Elgin, Scotland.

Family 4. **Acanthodidae.**

Fusiform or elongate-fusiform fishes, laterally compressed. A single dorsal fin. Free spines between paired fins usually absent, sometimes represented by one rudimentary pair. Lower Devonian to Lower Permian.

Mesacanthus Traquair (Fig. 76). A gracefully fusiform fish with slender spines. Pelvic fins not much smaller than the pectorals, about midway between these and the anal; a pair of minute spines between the paired fins. Dorsal fin more or less opposed to the anal, but not in advance of it. *Mesacanthus mitchelli* Egert. sp. (Fig. 76); *M. peachi* Egert. sp.; and *M. pusillus* Ag. sp., from the Lower and Middle Old Red Sandstone of Scotland. *M. affinis* Whiteaves sp., an equally small species from the Upper Devonian of Scaumenac Bay, Province of Quebec, Canada.

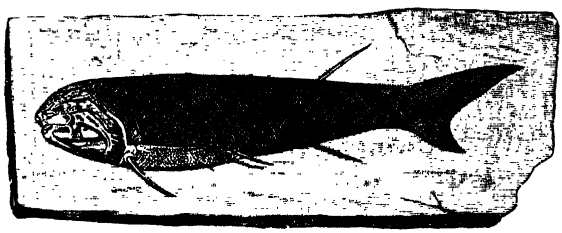


FIG. 76.

Mesacanthus mitchelli Eg. sp. Lower Old Red Sandstone; Farnell, Forfarshire. Nat. size (after Egerton).

Acanthodes Ag. (*Acanthoessus* Ag.; *Holacanthodes* Beyr.; *Protacanthodes* Fritsch) (Figs. 77, 78). A more elongated fish with similarly remote dorsal fin, but the pelvic fins relatively small and advanced forwards, the pectorals larger, and intermediate spines absent. Teeth minute or absent.

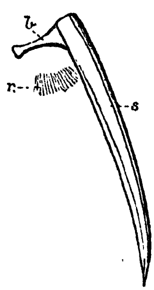


FIG. 77.

Acanthodes wardi Eg. Skeletal parts of pectoral fin, nat. size. Coal Measures; England. *b*, hollow basal element; *r*, dermal rays; *s*, dermal spine forming anterior border of fin (after A. S. Woodward).

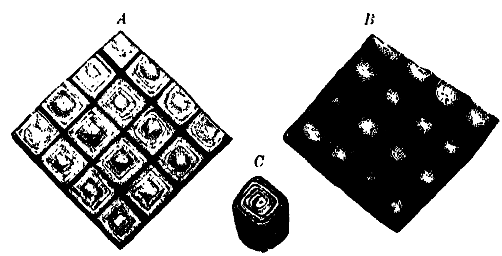


FIG. 78.

Acanthodes gracilis Beyr. Scales from the outer (*A*, *C*) and inner (*B*) aspects, much enlarged. Lower Permian; Germany.

Pectoral fin spine supported by a hollow, mesially constricted element (Fig. 77, *b*), which abuts against the side of its proximal end; a close series of short, fine dermal rays (*r*) sometimes appearing below this in the fin membrane. Scales smooth. Ranging throughout the Carboniferous in Scotland, the Coal Measures in England, North France, and North America, the Carboniferous

of Australia, and the Lower Permian in France, Germany, Bohemia, and Siberia. *A. bronni* Ag., the typical species, about 30 cm. in length, from the Rothliegendes of Rhenish Prussia (Lebach and Saarbrücken). *A. gracilis* Beyr. (Fig. 78), from Klein Neundorf, Silesia, probably identical with the latter. *A. wardi* Egert., from Coal Measures, Longton, Staffordshire. *A. lopatini* Rohon, from Permian, Siberia. *A. australis* A. S. Woodw., from Carboniferous, Victoria, Australia. *A.* (?) *concinnus* Whiteaves, from Upper Devonian, Scaumenac Bay, P.Q., Canada.

Traquairia Fritsch. As *Acanthodes* but without pelvic fins. *T. pygmaea* Fr., from Lower Permian Gas-Coal, Bohemia.

Cheiracanthus Ag. Like *Acanthodes*, but dorsal fin arising in advance of anal, and scales sculptured. *C. murchisoni* Ag., from Middle Old Red Sandstone, Scotland. Fragments from Lower Devonian of New Brunswick, Canada, and Upper Devonian of Granite Harbour, Antarctica.

Acanthodopsis Hancock and Atthey. Jaws with few large, laterally compressed, triangular teeth. *A. wardi* H. and A. from Coal Measures of Staffordshire, Northumberland, and Midlothian.

Eupleurogmus M'Coy. Carboniferous; Victoria, Australia.

Incertae Sedis.

Family 1. **Protodontidae.**

Teeth cuspidate, in transverse series curving round the cartilage of the jaw, those of each series fused together by their expanded bases. Upper Silurian and Lower Devonian.

Provisionally placed with the Acanthodians on account of the appearance of the top of the head, and the resemblance of the teeth of *Protodus* to the symphysial teeth of *Ischnacanthus*.

Protodus A. S. Woodw. (*Ancistrodus*, *Campylodus* Rohon). Dental crown a single conical cusp, which is solid or with very small pulp-cavity, and invested with ganodentine. *P. scoticus* E. T. Newton sp., known by imperfect head from Lower Old Red Sandstone, Forfarshire.[1] *P. jexi* A. S. Woodw. Lower Devonian; Campbellton, New Brunswick. Teeth from Isle of Oesel and Portugal.

Doliodus Traquair. Dental crown of three or more cusps in line, the outer larger than the intermediate cusps. *D. problematicus* A. S. Woodw. sp. Lower Devonian; Campbellton, New Brunswick.

Some minute teeth (*Palaeodus*, *Archodus* Rohon[2]) found mingled with Conodonts in the Ordovician near Petrograd may also belong to Acanthodians. They have a central pulp-cavity from which fine canaliculi pass into the dentine.

Order 2. PLEUROPTERYGII.[3]

Palaeozoic Elasmobranchs with persistent notochord and endoskeleton more or less calcified. Pterygoquadrate arcade movably articulated with the cranium. Paired

[1] *Woodward, A. S.*, Quart. Journ. Geol. Soc., vol. lxxi., Proc. p. lxvii., 1915.

[2] *Rohon, J. V.*, Bull. Acad. Imp. Sci. St.-Pétersb., vol. xxxiii., p. 269, 1889.

[3] *Cope, E. D.*, On *Symmorium*. Amer. Nat., 1893, p. 999, and Journ. Acad. Nat. Sci. Philad. [2], vol. ix., p. 427, 1894.—*Dean, Bashford*, Contributions to the Morphology of *Cladoselache*. Journ. Morphol., vol. ix., p. 87, 1894.—A new Cladodont from the Ohio Waverly. Trans. New

fins supported by unjointed, parallel radial cartilages, which may be partly fused at the base, but extend directly outwards to the edge of the fin membrane. Pelvic fins of male without claspers.

In the *Pleuropterygii* the vertebral axis seems to have remained unsegmented, and in the typical genus *Cladoselache* the tail is strongly heterocercal. The teeth are of the form commonly known as *Cladodus* (Fig. 80) in the Carboniferous formations, and several series must have been functional at one and the same time.

Family 1. **Cladoselachidae.**

Orbit surrounded by a ring of thin plates of dentine. Teeth cuspidate, with flattened expanded base. No dorsal fin spines. Caudal fin heterocercal. Upper Devonian and Carboniferous.

Cladoselache Dean (*Monocladodus* Claypole) (Fig. 79). The only well-defined genus hitherto discovered. The form is elongated and round-bodied, with a

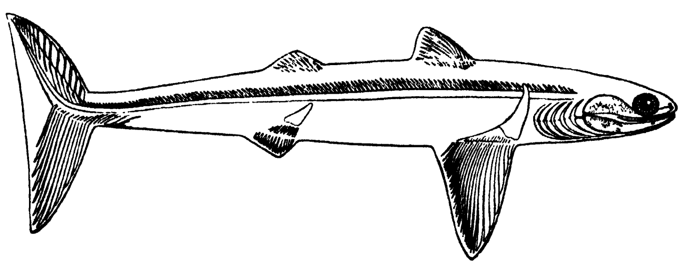


FIG. 79.
Cladoselache fyleri Newb. sp. Restored by Dean; about $^1/_8$ nat. size. Upper Devonian (Cleveland Shale); Ohio.

short blunt snout and forwardly placed eye. Circumorbital ring consisting of several series of thin, irregularly quadrangular small plates. Mouth terminal, and hyomandibular cartilage slender. Teeth largest, longest, and most acutely pointed at the symphysis of the jaw, smallest and shortest at the angle of the mouth. Each tooth with one principal cusp and a variable number of lateral cusps, fixed on the anterior border of a horizontally expanded base; the base of each tooth overlapped by its successor behind. Paired fins lappet-like, the pelvic pair with somewhat extended base line. Two low dorsal fins, without spine. Anal fin not yet observed. A short dermal expansion forming a horizontal keel on each side of the caudal pedicle just in advance of the strongly

FIG. 80.
Cladodus striatus Ag. Tooth, natural size. Carboniferous Limestone; Armagh, Ireland (after Davis).

York Acad. Sci., vol. xiii., p. 115, 1894.—The Finfold Origin of the Paired Limbs. Anat. Anz., vol. xi., p. 673, 1896.—Studies on Fossil Fishes. Mem. Amer. Mus. Nat. Hist. N. York, vol. ix., pt. 5, 1909.—*Fournier, G.*, and *Pruvost, P.*, Poissons élasmobranches du marbre noir de Denée. Mém. Soc. Géol. Nord, vol. ix., no. 2., 1928.—*Jaekel, O.*, Über die Beurteilung der paarigen Extremitäten. Sitzb. k. preuss. Akad. Wiss., vol. xxvi., p. 707, 1909 [on this see *Woodward, A. S.*, Proc. Linn. Soc., Sess. 133, p. 31, 1921].—*Pruvost, P.*, Description de *Denaea fournieri*. Bull. Acad. Roy. Belg., Cl. Sci., 1922, p. 213.—*Traquair, R. H.*, On *Cladodus neilsoni*. Trans. Geol. Soc. Glasgow, vol. xi., p. 41, 1897.

heterocercal caudal fin. Skin more or less armoured with minute lozenge-shaped denticles, which are apparently not enamelled. *C. kepleri*, *C. fyleri* Newb. sp., and other species sometimes nearly two metres in length, from the Cleveland Shale of Ohio.

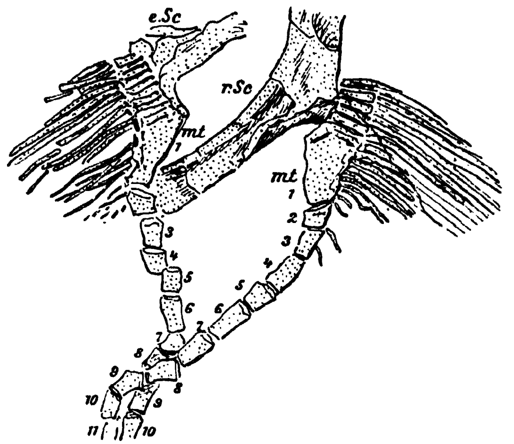


FIG. 81.

Cladodus neilsoni Traquair. Pectoral arch and fins. Lower Carboniferous (Calciferous Sandstone); Lanarkshire. *e.Sc*, *r.Sc*, left and right halves of pectoral arch; *mt*, metapterygium, with segments numbered 1-11. About $1/3$ nat. size (after Traquair).

The teeth termed *Cladodus* (Fig. 80) occur isolated in the Upper Devonian of Russia and Germany, and in the Lower Carboniferous of England, Scotland, Ireland, Belgium, Russia, India, and North America. They are also recorded from the Upper Carboniferous both of Europe and North America. These teeth, however, belong to genera of at least two families, and perhaps to other Orders besides the *Pleuropterygii*. *Cladodus neilsoni* Traq. (Fig. 81), from the Calciferous Sandstone of East Kilbride, Lanarkshire, is known by the imperfect head associated with a very remarkable pair of pectoral fins. *Symmorium reniforme* Cope, from the Coal Measures of Knox Co., Illinois, U.S.A., is a nearly similar fossil. *Denaea* (or *Denea*) *fournieri* Pruvost, from the Lower Carboniferous of Denée, Belgium, is also nearly related.

The genera *Dicentrodus* Traquair and *Phoebodus*, *Lambdodus* St. John and Worthen are founded on detached teeth from the Carboniferous Limestone, of uncertain affinities.

FIG. 82.

Ctenacanthus denticulatus M'Coy. $1/2$ nat. size. Carboniferous Limestone; Monaduff, Ireland (after M'Coy).

Family 2. **Ctenacanthidae.**[1]

No circumorbital plates. Teeth cuspidate, with flattened expanded base. A spine in front of each of the two dorsal fins. Upper Devonian to Lower Permian.

Ctenacanthus Agassiz (*Sphenacanthus* Agassiz) (Fig. 82). Dorsal fin spines laterally compressed, and the sides of their exserted portion ornamented with longitudinal ridges, which are usually crenulated or knotted, rarely smooth; their posterior face flattened or concave, with a series of small denticles along each margin. Anterior dorsal fin far forwards,

[1] *Dean, B.*, Mem. Amer. Mus. Nat. Hist., vol. ix., p. 242, 1909.

opposite the pectoral pair. *C. costellatus* Traquair[1] is represented by a nearly complete fish from the Lower Carboniferous (Calciferous Sandstone) of Eskdale, Dumfries, Scotland. *C. clarki* Newberry[2] is known by the head and anterior portion of trunk with the pectoral fins and anterior dorsal fin spine from the Upper Devonian (Cleveland Shale) of Ohio, U.S.A. *C. hybodoides* Egerton, perhaps of the same genus, is represented by fin spines and teeth in the English, Welsh, and Scottish Coal Measures. Numerous fin spines (*C. major* Ag., *C. denticulatus* M'Coy (Fig. 82), *C. angustus* Newb., etc.) from the Lower Carboniferous of Europe and from the Upper Devonian to Permian of North America.

Order 3. RHENANIDI.

Early Palaeozoic Elasmobranchs with ring-shaped vertebral centra. Cranial roof covered with dermal plates or tubercles, more or less fused together, and traversed by grooves for the sensory canals; mouth terminal; narial openings close together in the cranial roof between the orbits; a pineal foramen; a pair of large prominent occipital condyles. A pair of large clavicles meeting below in a wide symphysis. Pectoral fins supported by a few spaced, slender, segmented radial cartilages, which are not fused into plates at the base.

Family 1. Asterosteidae.[3]

Cranial roof covered with tuberculated dermal plates; orbits far forwards and directed upwards; the sensory canal forming a loop round the narial region. Trunk broad and depressed, with very large pectoral fins extending forwards to the middle of the head, small pelvic fins, and a small slender tail. Devonian.

Asterosteus Newberry. Known only by middle part of head shield, which is covered with stellate tubercles irregular in size and arrangement. *A. stenocephalus* Newb., with skull nearly 20 cm. long. Middle Devonian; Ohio and New York, U.S.A.

Gemuendina Traquair. Teeth apparently minute. Trunk gradually passing into the tail, which bears a small spinous dorsal fin but no caudal fin. Anterior vertebrae fused together, and directly supporting the scapular part of the pectoral arch. Dermal tubercles as in *Asterosteus*; separate longitudinal rows of small overlapping scutes on the tail. *G. stuertzi* Traq., known by nearly complete fishes about 25 cm. long. Lower Devonian; Bundenbach, Rhenish Prussia.

Family 2. Jagorinidae.[4]

Cranial roof covered apparently only with tubercles. Numerous small multicuspid teeth. Upper Devonian.

Jagorina Jaekel. Known by associated remains of cranium, teeth, and pectoral arch. *J. pandora* Jaekel. Upper Devonian; Wildungen, Germany.

[1] *Traquair, R. H.*, Geol. Mag., 1884, p. 3, pl. ii.—*Woodward, A. S.*, Proc. Linn. Soc., Sess. 133, p. 32, 1921.
[2] *Dean, B., loc. cit*, p. 249, pl. xxxiii., 1909.
[3] *Broili, F.*, Über *Gemündina stürtzi* Traquair. Abhandl. Bay. Akad. Wiss., math.-naturw. Abt., n.f., no. 6, 1930.—*Newberry, J. S.*, in Rep. Geol. Surv., Ohio, vol. ii., pt. ii., p. 35, 1875; also Palaeoz. Fishes, N. America, p. 45, 1889.
[4] *Jaekel, O.*, Schädelprobleme. Palaeont. Zeitschr., vol. iii., p. 217, 1921. See also *Stensiö E. A.*, Field Mus. Nat. Hist. Chicago, Publ. 232, p. 182, 1925, and Medd. om Grønland, vol. 86, no. 1, p. 30, 1931.

Order 4. STEGOSELACHII.

Late Palaeozoic Elasmobranchs with persistent notochord. Cartilage of cranial roof partly covered with (or enclosing) some symmetrically arranged ossifications. Pterygoquadrate arcade movably articulated with the cranium. No clavicular arch. Pectoral fins supported by parallel radial cartilages which are not fused at the base.

Family 1. **Cratoselachidae.**[1]

Cranial roof with a conical pineal plate, a pair of plates in front and two median plates behind. [*Dentition Unknown.*] Lower Carboniferous.

Cratoselache A. S. Woodward (Fig. 83). Known by associated cranial roof, cartilages of jaws, and pectoral arch. *C. pruvosti* A. S. Woodw. Lower Carboniferous; Denée, Belgium.

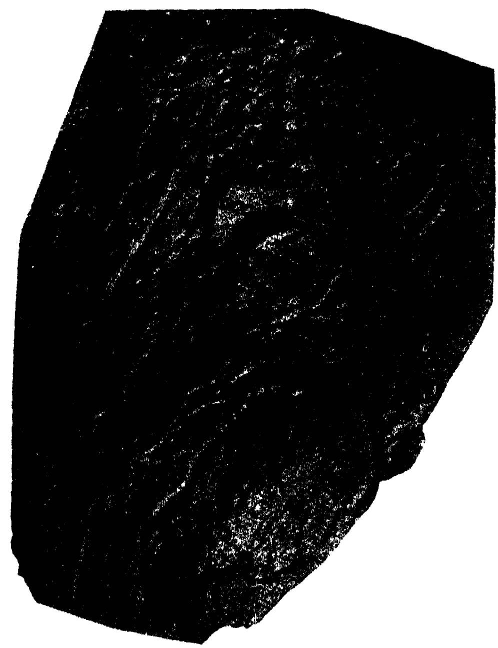


Fig. 83.

Cratoselache pruvosti A. S. Woodward. Parts of cranial roof, jaws, and pectoral arch. Lower Carboniferous; Denée, Belgium. *amd*, anterior median dorsal plate; b^1, ^{2}, basal cartilages of pectoral fin; *f*, rays of pectoral fin; *md*, rami of lower jaw; *occ*, median occipital plate; *pct*, pectoral arch; *pin*, pineal plate; *pro*, preorbital plates of cranial roof; *ptq*, rami of upper jaw (pterygoquadrates); *x*, undetermined. $^1/_2$ nat. size (after A. S. Woodward).

Order 5. ICHTHYOTOMI.[2]

(*Proselachii* Döderlein.)

Palaeozoic Elasmobranchs with endoskeleton well calcified, but no membrane calcifications. Pterygoquadrate arcade movably articulated with the cranium. No circumorbital plates. Five gill arches. Notochord persistent. Neural and haemal arches of vertebral axis long and slender. Pectoral fins with long, segmented axis from which smaller cartilages diverge on either side; pelvic fins of male with appended clasper; caudal fin diphycercal.

Family 1. **Pleuracanthidae.**

Body slender, but slightly depressed; mouth terminal. Teeth with two principal divergent cusps. Branchial arches provided with clusters of minute denticles. Dorsal fin elongate, low, continuous along the back from a point shortly behind the head; slender fin supports more numerous than the neural spines. Lower Carboniferous probably to Upper Triassic.

[1] *Woodward, A. S.*, *Cratoselache pruvosti* gen. et sp. nov., Livre Jubilaire, Soc. Géol. Belg., p. 59, 1924. See also *Fournier* and *Pruvost* in footnote, p. 57.

[2] *Beyrich, E.*, Über *Xenacanthus.* Monatsb. Berlin. Akad., 1848, pp. 24-33.—*Broili, F.*, Über *Diacranodus texensis* Cope. Neues Jahrb. f. Min., Beil.-Bd. xix., 1904.—*Brongniart, C.*, Bull. Soc. Industrie Min. (Saint-Étienne), sér. 3, vol. ii., livr. 4, 1888.—*Cope, E. D.*, Proc. Amer. Phil. Soc. 1884, p. 572.—*Davis, J. W.*, On the Fossil Fish-remains of the Coal Measures in the

The *Pleuracanthidae* occur in the coal-bearing strata of the Carboniferous system and in the Lower Permian of Europe and North America. One species is also known by a nearly complete skeleton from the Wianamatta Formation of New South Wales. For the isolated teeth of *Pleuracanthidae* various generic names have been proposed, e.g. *Diplodus* Ag., *Ochlodus*, *Aganodus*, *Pternodus* Owen, *Triodus* Jordan, *Thrinacodus* St. John and Worthen; for isolated spines, the generic names *Compsacanthus* Newberry, *Orthacanthus* Ag., and *Lophacanthus* Stock; for the clustered denticles of the branchial arches, the name *Stemmatias* Hay (*Stemmatodus* St. John and Worthen).

Pleuracanthus Ag. (*Diplodus* Ag.; *Triodus* Jordan; *Xenacanthus* Beyrich; ? *Didymodus* Cope; *Diacranodus* Garman; ? *Hypsospondylus* Jaekel) (Figs. 84-87). Head broad, semicircular in front, and provided behind with a long, slender dermal spine, which is hollow, either rounded in section or antero-posteriorly compressed, and bears a double longitudinal series of recurved

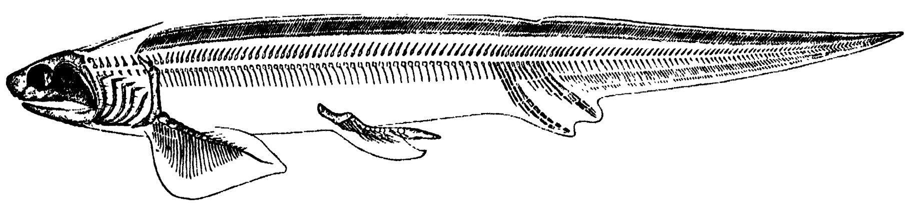


FIG. 84.

Pleuracanthus sessilis Jordan sp. Restoration by Jaekel, about $^1/_6$ nat. size. Lower Permian (Rothliegendes); Lebach, Rhenish Prussia.

denticles (Fig. 86). Teeth (Fig. 87) with two large divergent cusps fixed on a stout common base, and frequently a small third cusp between these (*Diplodus* Ag.). Five branchial clefts laterally placed in advance of the stout and broad, arched pectoral girdle, of which the two halves are fused ventrally but separated dorsally. Pectoral fins large, articulated with the postero-inferior angle of the pectoral girdle, and consisting of a segmented axis fringed on either side by cartilaginous rays. Pelvic supports in the form of a pair of separate triangular cartilages; basipterygium of pelvic fins segmented, fringed on one side with a series of cartilaginous rays, and continued behind into the clasper in the male. Two small anal fins, directly supported by the haemal arches. Caudal fin separated both from the anals and from the dorsal. Skin probably destitute of shagreen.

Complete skeletons are known from the Rothliegendes of Lebach, near Saarbrücken, in Rhenish Prussia (Fig. 84), and of Braunau (Fig. 85), in Bohemia, and Ruppersdorf, in Silesia; from the Lower Permian Gas-Coal of Bohemia; from the Coal Measures of Commentry in France; and from the

British Islands. I. Pleuracanthidae. Trans. Roy. Dublin Soc. [2], vol. iv., p. 703, 1893.—*Döderlein, L.*, Zool. Anzeig., vol. ii., p. 123, 1889.—*Fritsch, A.*, Fauna der Gaskohle, vol. ii. Prague, 1888–89.—*Goldfuss, A.*, Neues Jahrb., p. 404, 1847, and Beiträge zur vorweltlichen Fauna des Steinkohlengebirges, p. 23, pl. v., figs. 9, 10.—*Jaekel, O.*, Über die Organisation der Pleuracanthiden. Sitzungsb. Ges. naturf. Freunde, Berlin, 1895, p. 69.—Neue Rekonstruktion von *Pleuracanthus sessilis*. *Loc. cit.*, 1906, p. 155.—*Kner, R.*, Sitzungsb. k. Akad. Wiss. Wien, math.-naturw. Cl., vol. 55, p. 540, 1867.—*Koken, E.*, Über *Pleuracanthus* Ag. und *Xenacanthus* Beyr. Sitzungsb. Ges. naturf. Freunde, Berlin, 1889, p. 77.—*Reis, O. M.*, Das Skelett der Pleuracanthiden. Abhandl. Senckenberg. Naturf. Ges., vol. xx., p. 57, 1897.—Über permische Pleuracanthidenreste. Geogn. Jahreshefte, München, vol. xxvi., p. 155, 1913.—*Woodward, A. S.*, Mem. Geol. Surv. N.S. Wales, Palaeont., no. 10, p. 2, 1908.

Wianamatta Formation of New South Wales (*P. parvidens* A. S. Woodw.). Complete skulls have been found in the Coal Measures of Northumberland

Fig. 85.

Pleuracanthus (*Xenacanthus*) *decheni* Goldf. Lower Permian; Braunau, Bohemia. × $1/2$. *A*, anterior portion of fish. *B*, detached teeth, magnified (after F. Roemer).

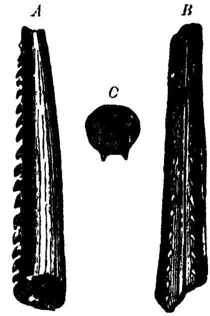


Fig. 86.

Pleuracanthus (*Orthacanthus*) *bohemicus* Fritsch. Lower Permian (Gas-Coal); Krotschow, Bohemia. *A*, side view. *B*, hinder view. *C*, transverse section. Natural size.

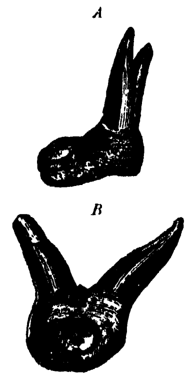


Fig. 87.

Pleuracanthus (*Diplodus*) *bohemicus* Quenst. Tooth in side view (*A*), and hinder view (*B*). Lower Permian (Gas-Coal); Nürschan, near Pilsen, Bohemia. Natural size.

and in the Permian of Texas (*Didymodus*, *Diacranodus*). Isolated teeth and spines are very abundant in the Carboniferous and Permian. Teeth resembling *Diplodus* occur in the Keuper of Somerset (*Triplodus* Moore, Proc. Geol. Assoc., vol. vi., p. 198, 1880; *Diplodus moorei* A. S. Woodward, Ann. Mag. Nat. Hist. [6], vol. iii., p. 299, 1889).

Anodontacanthus Davis. Dorsal spines without denticles. Carboniferous; England and Scotland.

Chondrenchelys Traquair. No dorsal spine. *C. problematica* Traq. Lower Carboniferous (Calciferous Sandstone); Dumfries, Scotland.

Order 6. SELACHII. Sharks and Skates or Rays.

Endoskeleton more or less calcified, but no membrane calcifications. Pterygoquadrate arcade movably articulated with the cranium. Gill clefts uncovered. Vertebral axis segmented in all but the earliest types. Paired fins with two or three short basal cartilages; pelvic fins of male with appended claspers.

Sub-Order 1. EUSELACHII.[1]

Teeth developed in numerous and rapid succession. Placoid scales (or shagreen) rarely fused into plates.

A. Branchial clefts lateral.
Sharks.

Family 1. **Edestidae.**[2]

Teeth Orodus*-like, but the symphysial row (perhaps sometimes double row) of teeth in each jaw much enlarged, laterally compressed, and fused into an arch, which either falls away at intervals or persists throughout life as a spiral.* Lower Carboniferous to Permian.

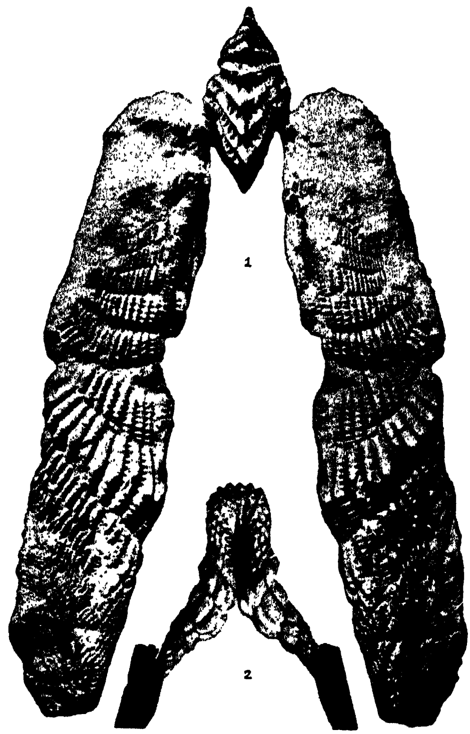


FIG. 88.

Campodus variabilis Newberry and Worthen sp. Lower dentition (1) compared with that of the existing *Cestracion* (2). Upper Carboniferous; Nebraska. 1/2 nat. size (after Eastman).

Campodus de Koninck[3] (*Agassizodus* St. John and Worthen; *Arpagodus* Trautschold) (Fig. 88). Symphysial teeth moderately compressed, with lateral extensions well developed and inclined forwards, buttressed at least on the anterior or outer face; root not much clasping the

[1] *Garman, S.*, The Plagiostomia (Sharks, Skates, and Rays). Mem. Mus. Comp. Zool. Harvard, vol. xxxvi., 1913.—*Jaekel, O.*, Die eocänen Selachier vom Monte Bolca. Berlin, 1894.—*Müller, J.*, and *Henle, F.*, Systematische Beschreibung der Plagiostomen. Berlin, 1841.—*Regan, C. T.*, A Classification of the Selachian Fishes. Proc. Zool. Soc., 1906, p. 722. Also *Alessandri, G. de*, Pesci terziarii del Piemonte. Mem. R. Accad. Sci. Torino [2], vol. xlv., 1895.—*Ihering, H. von*, Die miocäne Selachierfauna von Schwaben und ihre Beziehungen zu anderen Tertiärfaunen. Neues Jahrb. f. Min., etc., Beil.-Bd. 57, Abt. B, p. 466, 1927.—*Jaekel, O.*, Unter-tertiäre Selachier aus Südrussland. Mém. Com. Géol. St.-Pétersb., vol. ix., no. 4, 1895.—*Leriche, M.*, papers quoted on p. 3.—*Noetling, F.*, Die Fauna des samländischen Tertiärs. Abhandl. geol. Specialk. Preussen, vol. vi., pt. 3, 1885.—*Probst, J.*, Beiträge zur Kenntniss der fossilen Fische aus der Molasse von Baltringen. Württemb. naturw. Jahresh., 1874, 1877, 1878, and 1882.—*Stromer, E.*, Wirbeltierreste der Baharije-Stufe (unterstes Cenoman). Die Plagiostomen. Abh. Bay. Akad. Wiss., math.-naturw. Abt., vol. xxxi., no. 5, 1927.—*White, E. I.*, papers quoted on p. 3.—*Woodward, A. S.*, Some fish-remains from the Paraná Formation, Argentine Republic. Ann. Mag. Nat. Hist. [6], vol. vii., p. 1, 1900.

[2] *Hay, O. P.*, An important specimen of *Edestus*. Proc. U.S. Nat. Mus., vol. xlii., p. 31, 1912.—*Woodward, A. S.*, A new species of *Edestus*. Quart. Journ. Geol. Soc., vol. lxxii., p. 1, 1916.

[3] *Eastman, C. R.*, Bull. Mus. Comp. Zool. Harvard, vol. xxxix., pp. 57, 184, 1903.—*Lohest, M.*, Ann. Soc. Géol. Belg., vol. xi., p. 305, 1883.

next tooth; the fused teeth falling away at intervals. Small lateral teeth buttressed on the outer, often also on the inner face. *C. variabilis* Newb.

FIG. 89.
Edestus crenulatus Hay. Upper Carboniferous; Illinois. $^2/_5$ nat. size (after Hay).

and Worth. sp. (Fig. 88) from Coal Measures, U.S.A. Other species from Lower Carboniferous of England and Belgium, and from Upper Carboniferous, Mjatschkowa, Moscow.

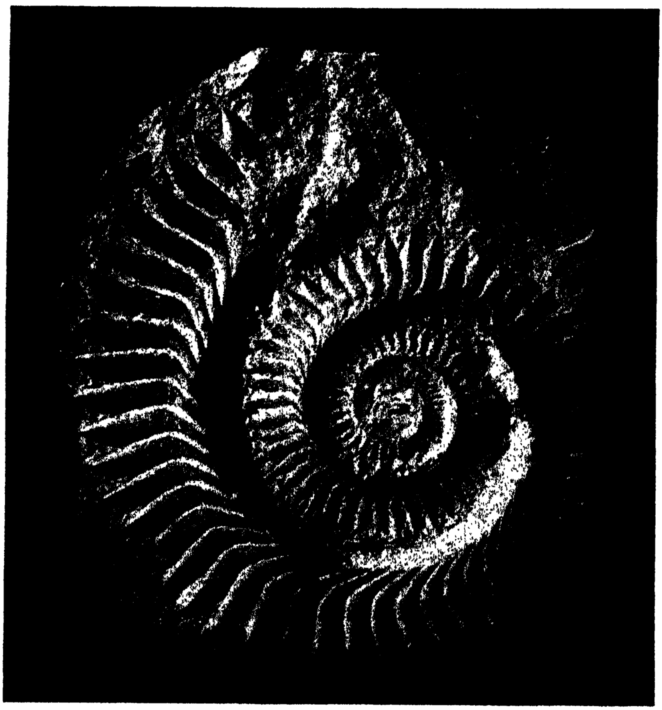


FIG. 90.
Helicoprion bessonowi Karpinsky. Permo-Carboniferous (Artinskian); Perm. $^1/_2$ nat. size (after Karpinsky).

Edestus Leidy (Fig. 89). Symphysial teeth much laterally compressed, serrated, with lateral extensions greatly reduced and inclined backwards; root large and deeply clasping next tooth; the fused teeth falling away at intervals. Small lateral teeth as in *Campodus*. *E. vorax* Leidy, *E. minor* Newberry, *E. mirus, crenulatus* Hay, from Coal Measures, U.S.A., *E. newtoni* A. S. Woodw., from Millstone Grit, Yorkshire. Other species from Upper

Carboniferous, Moscow, and marine bands in the English and South Welsh Coal Measures.

Toxoprion Hay.[1] Symphysial teeth much laterally compressed, serrated, with lateral extensions much reduced and inclined forwards; teeth of young relatively broad and large. *T. lecontei* Dean sp. Coal Measures; Nevada, U.S.A.

Helicoprion Karpinsky [2] (*Campyloprion* Eastman; *Lissoprion* Hay) (Fig. 90). Symphysial teeth much laterally compressed, serrated, with small lateral extension inclined forwards; root small but firmly clasping next tooth; the fused teeth persisting throughout life and forming a spiral. *H. bessonowi* Karp. (Fig. 90) from Permo-Carboniferous, Perm (Russia) and Japan. Other species of same age from Russia, U.S.A., Canada (Alberta), India, and West Australia.

Parahelicoprion Karpinsky. Intermediate between *Campodus* and *Helicoprion*. Probably with dermal spines named *Xystracanthus* Leidy. Permo-Carboniferous; Krasnoufimsk, Ural.

According to H. Schmidt,[3] the dentition of *Dicrenodus* Romanowsky (*Carcharopsis* Davis, *Pristicladodus* M'Coy), from the Lower Carboniferous of Russia, Germany, Scotland, England, Ireland, and North America, is arranged on the same plan as that of *Edestus*, except that the enlarged symphysial teeth are in double series and not fused together. *Hybodopsis* W. J. Barkas, from the English Coal Measures, and *Mesodmodus*, *Hybocladodus* St. John and Worthen, from the Lower Carboniferous of Iowa and Illinois, U.S.A., may be related.

Family 2. **Hybodontidae.**[4]

Teeth numerous, mostly obtuse, never fused into continuous plates; several series simultaneously in function. Notochord persistent. Some ribs long and slender; neural arches also long and slender. Each of the two dorsal fins armed with a spine, which is as deep as the fin; the spine ornamented on the sides and bearing one or two rows of posterior denticles. Anal fin without spine. Tail heterocercal. Paired hooked head spines often present. Devonian or Lower Carboniferous to Cretaceous.

? *Protacrodus* Jaekel. Upper Devonian; Wildungen, Germany.

? *Eoörodus* Branson. Upper Devonian; Missouri, U.S.A.

Orodus Ag. (*Scoliorhiza* Raymond) (Fig. 91), known only by obtuse elongated teeth. The dental crown raised in the middle, and its surface marked with more or less prominent wrinkles, which rise from each long margin or from a median longitudinal crest. Base of tooth very stout. *O. ramosus* Ag. (Fig. 91), and other species from the Carboniferous Limestone of Britain and Belgium, and the Carboniferous of Russia. Also numerous species in corresponding American formations, one specimen said to show

[1] *Hay, O. P.*, Proc. U.S. Nat. Mus., vol. xxxvii., p. 56, 1909.

[2] *Karpinsky, A.*, Verhandl. K. Russ. Min. Ges., St. Petersb. [2] vol. xxxvi., p. 361, 1899; vol. xlix., p. 83, 1912.—Bull. Soc. Oural. Sci. Nat. Ekaterinebourg, vol. xxxv., p. 117, 1915.—Bull. Acad. Imp. Sci. St.-Pétersb., 1916, p. 701.—Sur une nouvelle trouvaille de restes de *Parahelicoprion*, et sur les relations de ce genre avec *Campodus*. Livre Jubilaire, Soc. Géol. Belg., p. 127, 1924.

[3] *Schmidt, H.*, Ein den Edestiden ähnliches Haigebiss aus dem Kulm des Harzes. Palaeont. Zeitschr., vol. xi., p. 82, 1929.

[4] *Jaekel, O.*, Die Selachier aus dem oberen Muschelkalk Lothringens. Abh. geol. Specialkarte Elsass-Lothringen, vol. iii., pt. iv., 1889.—Über *Hybodus* Ag. Sitzb. Ges. naturf. Freunde, Berlin, 1898, p. 135.

a dorsal fin spine resembling *Ctenacanthus* Ag. One species in Alberta, Canada.

Tristychius Ag.[1] (*Ptychacanthus* Ag.) (Fig. 92). Dorsal fin spines with a few sharp longitudinal ridges distally, three only—one upon the front margin and one on each side—extending far downwards in the type species. Teeth of shape named *Lophodus* Romanowsky. *T. arcuatus* Ag. Lower Carboniferous; Scotland.

Wodnika Münster (Fig. 93).[2] Large gently, rounded, smooth crushing teeth. Dorsal fin spine with coarse longitudinal ridges. *W. striatula* Münst. (Fig. 93), from Kupferschiefer, Thuringia and Hesse, and Marl Slate, Durham.

Lophodus Symonds. Teeth hollow with relatively thick layer of ganodentine; lateral teeth elongated,

FIG. 91.
Orodus ramosus Ag. Carboniferous Limestone; Armagh. 1/2 nat. size (after Davis)

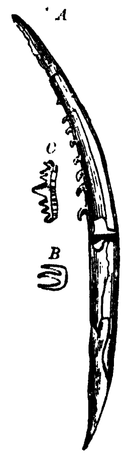


FIG. 92.
Tristychius arcuatus Ag. Dorsal fin spine (*A*), shagreen-scale (*B*), and tooth (*C*), about natural size. Lower Carboniferous; Scotland (after Stock).

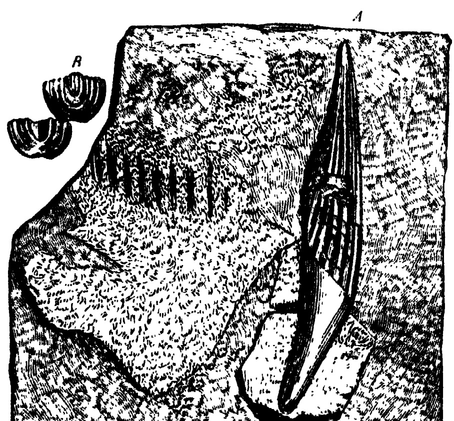


FIG. 93.
Wodnika striatula Münst. Enlarged. Kupferschiefer; Riechelsdorf, Hesse. *A*, Fin spine. *B*, Shagreen granules.

compressed, and keeled; symphysial teeth tricuspid. Dorsal fin spines as in *Hybodus*, but denticles between posterior keel and edges. *L. keuperinus* Murch. and Strickl. sp. (= *Phoebodus brodiei* A. S. W.). Keuper; England.

Nemacanthus Ag. (*Desmacanthus* Quenstedt). Dorsal fin spines with enamelled keel on front edge, sides more or less tuberculated, and a row of small denticles along each edge of the posterior face. *N. monilifer* Ag. Rhaetic; England, France, and Würtemberg. Other species in the German Muschelkalk and in the Triassic of N. Italy, Spitzbergen, and Idaho, U.S.A. *N. brevis* Phillips, Stonesfield Slate.

Hybodus Ag.[3] (*Meristodon* Ag.; *Polyacrodus*, *Orthybodus*, *Parhybodus* Jaekel) (Figs. 94, 95). Teeth and dorsal fin spines almost as in *Ctenacanthus*, but

[1] *Woodward, A. S.*, Quart. Journ. Geol. Soc., vol. lxxx., p. 338, 1924.
[2] *Weigelt, J.*, Leopoldina (Halle), vol. vi., p. 602, 1930.
[3] For literature see *Koken, E.*, Über *Hybodus*. Palaeont. Abhandl., f.n., vol. v., 1907, and *Woodward, A. S.*, Wealden and Purbeck Fishes. Mon. Palaeont. Soc., 1916.

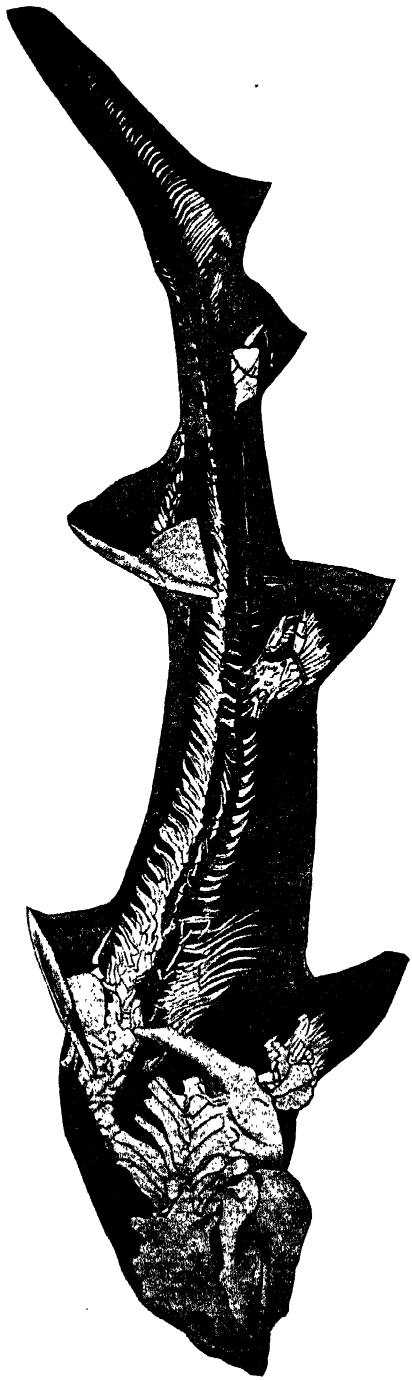


Fig. 94.
Hybodus hauffianus E. Fraas. Skeleton with skin. Upper Lias: Holzmaden, Wurtemberg. About $^1/_{10}$ nat. size (after Koken).

double series of denticles on hinder face of fin spine median, not laterally placed. Symphysial teeth few and relatively large. The greater part of the dental crown consisting of vasodentine. One or two large hook-shaped, semi-barbed dermal spines (*Sphenonchus*) immediately behind each orbit, at least in the male. Shagreen sparse, consisting of small conical, radiately grooved tubercles, which are sometimes fused into groups of three. Numerous species ranging from the Trias to the Lower Cretaceous. Teeth of *H. plicatilis* Ag. (Fig. 95, *A*), abundant in the Muschelkalk, allied species in the Trias of Spitzbergen. Nearly complete skeletons from the Lower Lias of England (*H. delabechei* Charlesworth; *H. reticulatus* Ag., Fig. 95, *B*), the Upper Lias of Würtemberg (*H. hauffianus* Eb. Fraas) (Fig. 94), and the Lithographic Stone (Upper Jurassic) of Bavaria (*H. fraasi* Brown). Fine skulls from Wealden, Pevensey Bay, Sussex (*H. basanus* Egert.). Portions of skeleton also from the Upper Beaufort Beds of Orange River Colony, S. Africa (*H. africanus* Broom), and from the Kimmeridgian of Lérida, Spain (*H. woodwardi* Vidal).

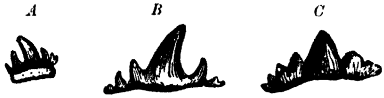


Fig. 95.

Teeth of *Hybodus*. *A*, *H. plicatilis* Ag. Muschelkalk; Laineck, near Bayreuth. *B*, *H. reticulatus* Ag. Lower Lias; Lyme Regis, Dorset. *C*, *H. polyprion* Ag. Lower Oolite (Stonesfield Slate); Stonesfield, Oxfordshire.

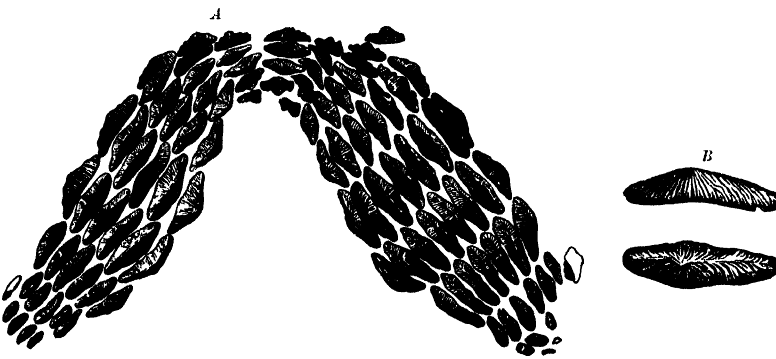


Fig. 96.

Acrodus anningiae Ag. Dentition, 1/3 natural size. Lower Lias; Lyme Regis. *A*, Symphysis. *B*, Detached tooth, seen from side and above, natural size.

Acrodus Ag. (*Thectodus* Plieninger; *Leiacanthus* Ag.) (Fig. 96). A genus only differing from *Hybodus* in the rounded, non-cuspidate character of the teeth. Common in the Triassic and Jurassic, and ranging to the Upper Cretaceous. *A. gaillardoti* Ag., teeth from Bunter, Muschelkalk, and Keuper of Germany and France. *A. minimus* Ag., common in European Keuper and Rhaetic, allied species in the Trias of California, U.S.A., and Spitzbergen. *A. anningiae* Ag. (Fig. 96), and *A. nobilis* Ag., known by fine specimens from the Lower Lias, Lyme Regis. *A. levis* A. S. Woodw., teeth from English Gault.

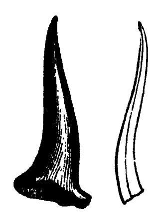


Fig. 97.

Orthacodus longidens Ag. sp. White Jura γ; Böllert, Würtemberg.

Orthacodus A. S. Woodw. (*Sphenodus* Ag. *nec* Gray, *nec* Lund) (Fig. 97). Teeth very slender and erect, compressed, without lateral denticles; the root broad and depressed, simple. *O. longidens* Ag. sp. (Fig. 97) and other species

are Upper Jurassic. Apparently also Cretaceous (*Oxyrhina lundgreni* J. W. Davis, Trans. Roy. Dublin Soc., n.s., vol. iv., p. 393, 1890).

Palaeobates Meyer. Teeth depressed, rounded, without lateral denticles and not keeled; the crown consisting of dentine in which the fine tubules radiate from a small central pulp cavity. Trias of Europe and Spitzbergen.

Bdellodus Quenstedt. All teeth quadrate, with slightly arched but flattened crown, superficially ornamented with reticulate markings. Three paired series of square symphysial teeth, one pair of elongated lateral teeth. *B. bollensis* Quenst., from Upper Lias, Würtemberg. "*Strophodus thiollierei*" Dumortier. Middle Lias; France.

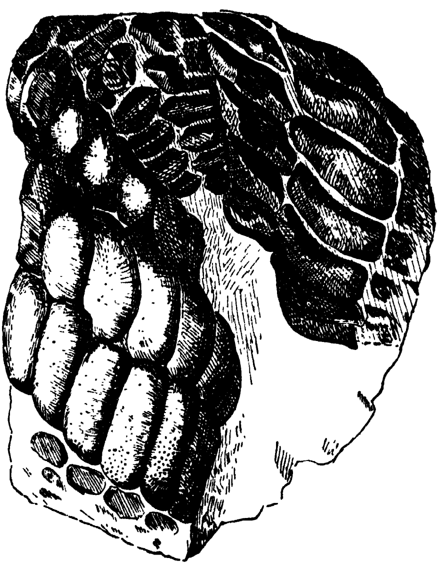


FIG. 98.
Asteracanthus (*Strophodus medius* Owen). Lower dentition. Lower Jurassic (Bathonian); Caen, Normandy. $1/2$ nat. size (after Owen).

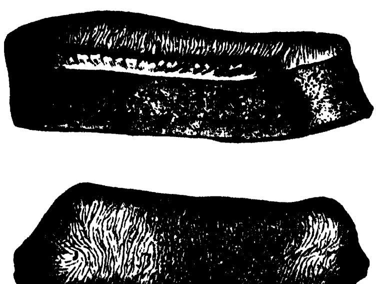


FIG. 99.
Tooth of *Asteracanthus* (*Strophodus reticulatus* Ag.), in side view and upper view. Corallian; Tonnerre, Yonne. Nearly nat. size.

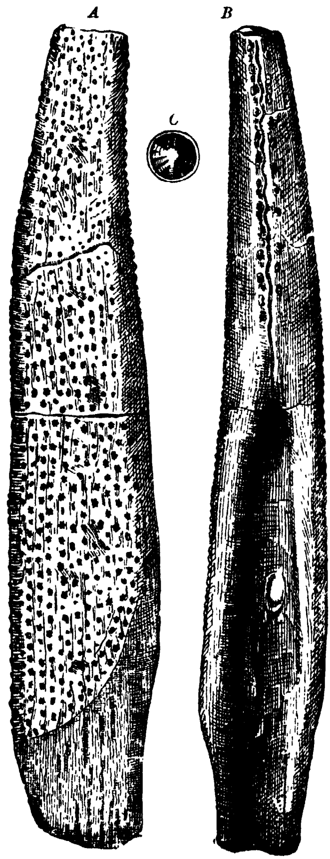


FIG. 100.
Asteracanthus ornatissimus Ag. Dorsal fin spine, lateral view (*A*), posterior view (*B*), and detached tubercle enlarged (*C*). Portlandian; Soleure, Switzerland.

Asteracanthus Ag. (*Strophodus* Ag.; *Curtodus* Sauvage) (Figs. 98-100). Principal teeth elongated, irregularly quadrate, with slightly arched but

flattened crown; symphysial teeth few, smaller but relatively large, much arched, without lateral denticles, and longitudinally keeled; all superficially marked by reticulating ridges (Figs. 98, 99). Head spines as in *Hybodus* and *Acrodus*, but one pair smaller than the other. Dorsal fin spines (Fig. 100)

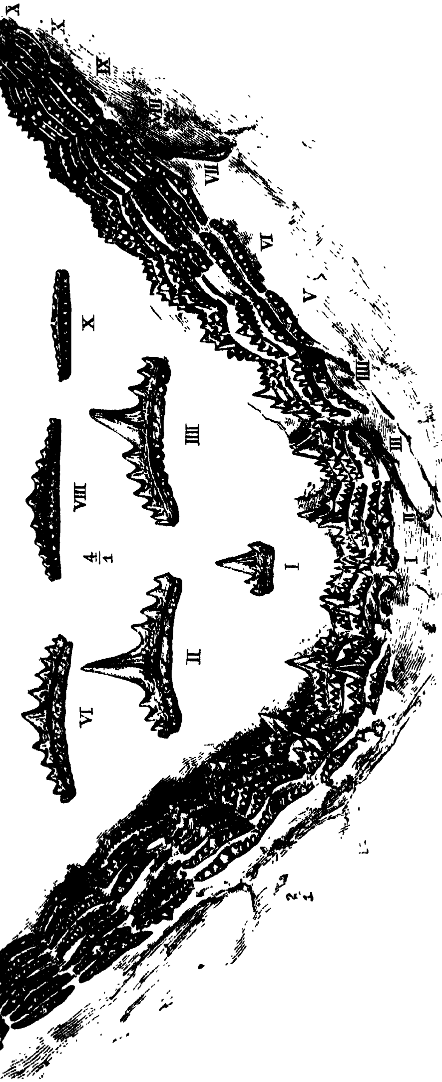


FIG. 101.

Synechodus dubrisiensis Mackie sp. Dentition, twice nat. size, with six teeth enlarged four times. Lower Chalk; Sussex (after A. S. Woodward).

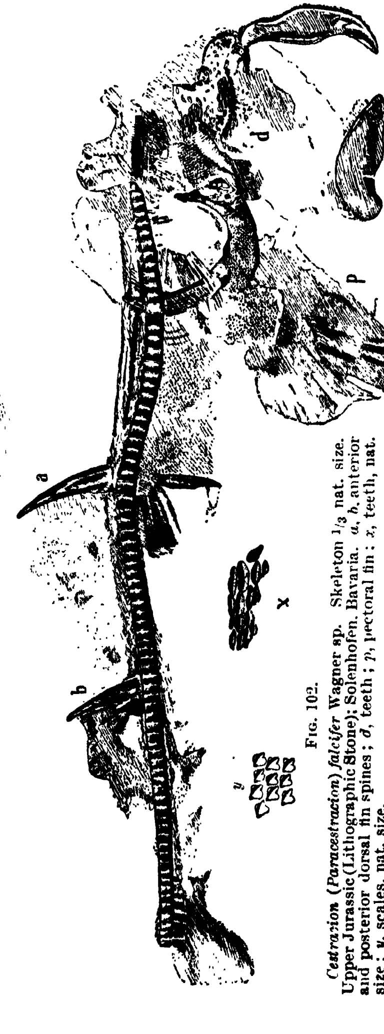


FIG. 102.

Cestracion (*Paracestracion*) *falcifer* Wagner sp. Skeleton $1/3$ nat. size. Upper Jurassic (Lithographic Stone); Solenhofen, Bavaria. *a*, *b*, anterior and posterior dorsal fin spines; *d*, teeth; *p*, pectoral fin; *x*, teeth, nat. size; *y*, scales, nat. size.

marked by stellate tubercles, sometimes partly fused into longitudinal ribs; also bearing a median longitudinal double series of tubercles on their hinder face. Lower, Middle, and Upper Jurassic. *A. ornatissimus* Ag. (*Strophodus reticulatus* Ag.) (Figs. 99, 100), well known from Corallian, Oxfordian, and Kimmeridgian of Europe. *Strophodus magnus* Ag. English and French Lower

Oolites. Teeth also found in Prov. Iwaki, Japan, and in Madagascar. A doubtful tooth from Upper Trias, California (*Strophodus shastensis* H. C. Bryant, Bull. Dept. Geol. Univ. California, vol. viii., p. 27, 1914).

Family 3. **Cestraciontidae.**

Teeth as in Hybodontidae. *Vertebral centra cyclospondylic or asterospondylic. Ribs and neural arches very short and broad. Each of the two dorsal fins armed with a spine which is less deep than the fin; the spine almost or completely unornamented and without posterior denticles. Anal fin without spine. Tail heterocercal. No head spines.* Lower Jurassic to Recent.

Palaeospinax Egerton (*Aulakisanthus* Terquem and Piette).[1] Dentition comparatively specialised; the few anterior teeth high-crowned and prehensile, with a single pair of lateral denticles; posterior teeth low-crowned, with two or three pairs of lateral denticles reduced to minute beads. Vertebrae very slightly asterospondylic. Dorsal fin spines smooth and enamelled, sometimes with a few tubercles at the base. Shagreen fine and dense. *P. priscus* Egert., known by nearly complete specimens from Lower Lias, Lyme Regis. Fragments of other species from Upper Lias, Würtemberg, and Lower Lias, France.

FIG. 103.
Lower Jaw of Recent Port Jackson Shark, *Cestracion philippi* Cuv. Australia. 2/3 nat. size.

Synechodus A. S. Woodward (*Molobrosichthys* Ameghino) (Fig. 101). Almost identical with *Palaeospinax*, but teeth with more numerous lateral denticles, and vertebrae more distinctly asterospondylic. Complete jaw of *S. dubrisiensis* Mackie sp. (Fig. 101), and greater part of skeleton of same species known from the Lower Chalk of England. Tail of *S. ejuncidus* Lambe sp., from Edmonton Formation, Red Deer River, Alberta, Canada (Ottawa Naturalist, 1918, p. 27). Teeth of other species from various Cretaceous formations in Europe and N. Africa, Cretaceo-Tertiary of New Zealand, Chile, and Patagonia. One (*S. clarki* Eastman) from the Maryland Eocene, and others from Lower Eocene of France and Belgium.

Cestracion Cuv. (*Heterodontus* Blainv.; *Drepanephorus* Egert.; *Pseudacrodus* Amegh.; *Paracestracion* Koken) (Figs. 102, 103). Symphysial teeth small, numerous and prehensile, with a median cusp and one pair of lateral denticles; lateral teeth in oblique series, with faintly keeled and finely rugose crown. Vertebrae asterospondylic. Dorsal fin spines smooth. Nearly complete skeletons from the Lithographic Stone (Upper Jurassic) of Bavaria (*C. falcifer*

[1] *Dean, B.*, Mem. Amer. Mus. Nat. Hist., vol. ix., p. 254, 1909.

Wagn. sp., Fig. 102) and the Chalk of England (so-called *Drepanephorus canaliculatus* Egert.). An immature fish, with the usual cuspidate teeth, from the Lithographic Stone of Bavaria, is named *C. zitteli* Eastman (Amer. Journ. Sci. [4], vol. xxxi., p. 401, 1911). Teeth from Lower and Middle Eocene of England and Belgium, and from the Lower Tertiary of Patagonia, New Zealand, and Australia. Existing in Australian and other seas.

Family 4. **Notidanidae.**

Teeth with one or more sharply pointed cusps, usually laterally compressed; root not forked. Six or seven pairs of gill clefts. Notochord largely persistent, and vertebral centra incomplete. A single unarmed dorsal and anal fin, and a large heterocercal caudal fin. Middle Jurassic to Recent.

Notidanus Cuv. (*Hexanchus, Heptanchus* Müller and Henle; *Notidanion* Jordan and Hannibal) (Figs. 104, 105). Principal teeth consisting of a series of compressed cusps fixed on a long base; all the cusps inclined in one direction, the anterior larger than the others, with or without small denticles at its base in front. Anterior teeth of the upper jaw clustered, awl-shaped; a median or symphysial series in the lower jaw. Principal teeth of the upper jaw less laterally elongated, with fewer cusps than those of the lower jaw. Range from Middle Jurassic to present day. *N. muensteri* Ag., represented by a complete skeleton from the Lithographic Stone (Lower Kimmeridgian) of Solenhofen, Bavaria, and *N. gracilis* Davis, by a smaller skeleton from the Upper Cretaceous of Sahel Alma, Mount Lebanon. Detached teeth from the Oxford Clay of England and Corallian of Würtemberg; from the Chalk of England (*N. microdon* Ag.) and the Cretaceous of Madagascar and New Zealand (*N. dentatus* A. S. Woodw.); and numerous species from Tertiary formations (e.g. *N. primigenius* Ag., Fig. 105).

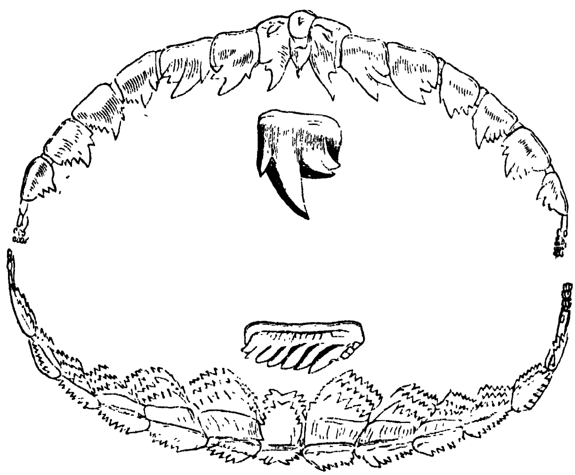


FIG. 104.
Dentition of the Recent Indian Grey Shark, *Notidanus* (*Heptanchus*) *indicus*.

FIG 105.
Notidanus primigenius Ag. Lower tooth. Oligocene; Weinheim, Hesse Darmstadt. Natural size.

Xenodolamia Leidy (*Xiphodolamia* Leidy).[1] Lateral teeth with a single broad laterally compressed cusp. *X. simplex* Leidy, from Ashley River Phosphate Beds, South Carolina. *X. eocaena* A. S. Woodw. sp., from Eocene, England and Belgium.

[1] *Leriche, M.*, Mém. Mus. Roy. Hist. Nat. Belg., vol. iii., p. 183, 1905.

Chlamydoselache Garman. Teeth with broad, backwardly extended base, and the crown consisting of three slender, curved, subconical cusps, which are separated by a pair of rudimentary denticles. Wide distribution in existing deep sea. Isolated teeth in Pliocene of Tuscany (*C. lawleyi* Davis, Proc. Zool. Soc., 1887, p. 542), and in the Oligocene or Miocene of Trinity Island, Lesser Antilles (*C. tobleri* Leriche, Bull. Soc. Belge Géol., etc., vol. xxxviii., p. 56, 1929).

Family 5. **Protospinacidae.**[1]

As Spinacidae, but a small anal fin present. Upper Jurassic.

Protospinax A. S. Woodw. Teeth small, compressed to a sharp edge. Pectoral fins extending as far backwards as the pelvic pair. Anterior dorsal fin spine opposite pelvic fins. Anal fin very small and remote; caudal fin not notched. Shagreen dense and fine; lateral line supported by calcified rings as in Chimaeroids. *P. annectens* A. S. Woodw. Upper Jurassic (Lithographic Stone); Eichstädt, Bavaria.

[*Rhadamas* Münster, from the German Kupferschiefer, is also considered by Jaekel[2] to be related to the ancestry of the *Spinacidae* and may represent a separate family, the *Rhadamantidae*. Rostrum elongated; pectoral fin much resembling that of *Acanthias*.]

Family 6. **Spinacidae** (*Squalidae*). Spiny dog-fishes.

Body fusiform to trihedral, somewhat depressed. Mouth gently arched; snout obtuse. Gill clefts small; spiracles large, behind the eye. Pectoral fins not notched at their origin and not produced forwards; the two dorsal fins often armed with a spine; anal fin absent; caudal fin heterocercal. Upper Cretaceous to Recent.

Centrophorus Müller and Henle (Fig. 106). Dorsal fin spines present. Upper teeth erect, triangular, or narrow lanceolate, with a single cusp; lower

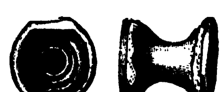


FIG. 106.

Vertebra (central double-cone) of *Centrophorus*. Upper Cretaceous; Maastricht (after Hasse).

FIG. 107.

Acanthias radicans Probst. Tooth, × 2. Miocene (Molasse); Baltringen, Würtemberg (after Probst).

FIG. 108.

Scymnus triangulus Probst. Tooth, × 2. Miocene (Molasse); Baltringen (after Probst).

teeth triangular and compressed, with the apex much turned aside. Upper Cretaceous, Sahel Alma, Mount Lebanon (*Spinax primaevus* Pictet). Tertiary and Recent.

Acanthias Risso (*Squalus* Linn.; *Centrophoroides* Davis) (Fig. 107). As *Centrophorus*, but teeth in upper jaw as in lower jaw. Upper Cretaceous, Sahel Alma, Mount Lebanon (*Centrophoroides latidens* Davis). Tertiary (*A. radicans* Probst) and Recent.

Isistius Gill. Upper Cretaceous; Egypt. Eocene; Belgium.

Centrina Cuv. Pliocene and Recent.

[1] *Woodward, A. S.*, Proc. Zool. Soc., 1918, p. 232.

[2] *Jaekel, O.*, 17. Jahresb. Niedersächsisch. geol. Vereins, Hannover, p. 182, 1925.—For another interpretation see O. M. Reis, Geogn. Jahresh., vol. xxvi., p. 157, 1913.

Scymnus Cuv. (Fig. 108). No dorsal fin spines. Upper teeth small, pointed; lower teeth much larger, broad and compressed, triangular, erect or only slightly inclined laterally. Miocene to Recent.

Echinorhinus Blainv. (*Goniodus* Ag.). Miocene to Recent.

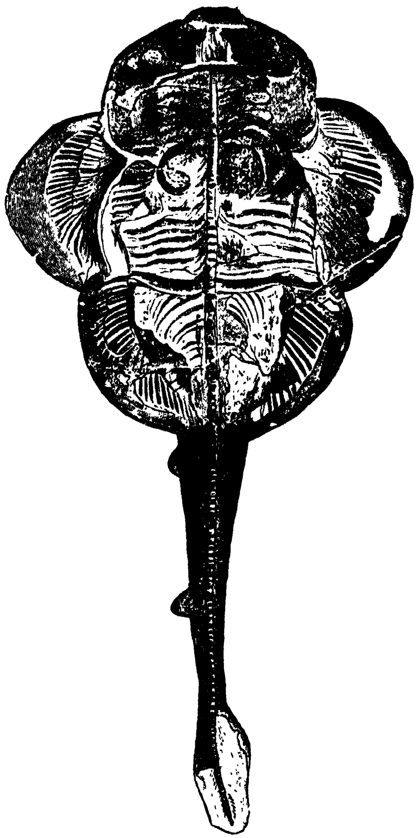


FIG. 109.

Squatina alifera Münst. sp. Upper Jurassic; Eichstadt, Bavaria. (Original over one metre long, in Palaeontological Museum, Munich.)

Family 7. **Pristiophoridae.**[1]

Trunk fusiform. Snout much elongated and flattened, without lateral cartilages, but usually fringed on each border with pointed dermal teeth. Five or six pairs of gill clefts. Vertebrae cyclospondylic. Pectoral fins not extending forwards. The two dorsal fins without spines; anal fin absent; caudal fin diphycercal. Upper Cretaceous to Recent.

Propristiophorus A. S. Woodward. Snout without lateral teeth. *P. tumidens* A. S. W., from Upper Cretaceous, Sahel Alma, Mount Lebanon.

Pristiophorus M. and H. Rostral. Teeth of unequal length, not serrated. Miocene to Recent.

Pliotrema Regan. With six gill clefts. Rostral teeth serrated. Tertiary; New Zealand. Recent; Indian Ocean.

A rostrum, 17·5 cm. long, in some respects resembling that of *Pristiophorus* but without lateral teeth, has been found in the Rhaetic of the Bavarian Alps (*Raineria* Osswald). Its affinities are uncertain.[2]

Family 8. **Squatinidae.** Angel-fishes or Monk-fishes.

Trunk broad and depressed. Vertebrae tectospondylic (Fig. 111). *Teeth pointed and conical, without lateral denticles, on depressed root; several series in function. Pectoral fins large, separated by a cleft from the head, so that the gill openings are still directed laterally. Two dorsal fins on the tail, without spines; anal fin absent; caudal fin scarcely heterocercal. Skin covered with small placoid scales.* Jurassic to Recent.

Squatina Aldrovandi (*Rhina* Klein; *Thaumas* Münst.; *Phorcynis* Thioll.; *Scaldia* Le Hon; *Trigonodus* Winkler; *Pseudorhina* Jaekel) (Figs. 109-111) first appears in the Upper Jurassic and survives in the existing fauna. Complete skeletons of *S. alifera* Münst. sp. (Figs. 109, 110); *S. speciosa* Meyer;

[1] *Jaekel, O.*, Über die systematische Stellung und über fossile Reste der Gattung *Pristiophorus.* Zeitschr. Deutsch. Geol. Ges., 1890, p. 86; also Archiv f. Naturgesch., 1891, p. 15.

[2] *Osswald, K.*, *Raineria* nov. gen., ein Selachier-Rostrum aus dem alpinen Rhät. Zeitschr. Deutsch. Geol. Ges., vol. lxxx. A. Abh., p. 496, 1928.

and *S. acanthoderma* Fraas, occur in the Lithographic Stone of Bavaria and Würtemberg (Nusplingen); and the genus is also represented in the

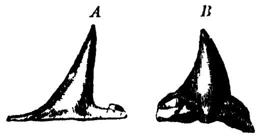


FIG. 110.

A, *Squatina alifera* Münst. sp. Tooth, × 2. Upper Jurassic (Lithographic Stone); Solenhofen. *B*, *Squatina fraasi* Probst. Tooth, × 2. Miocene (Molasse); Baltringen.

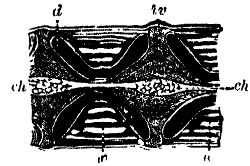


FIG. 111.

Longitudinal section of the tectospondylic vertebral column of *Squatina angelus* Linn. *ch*, notochord; *d*, calcified double-cone (basis of centrum); *iv*, intervertebral space; *w*, vertebral centra with concentric calcified rings (after Hasse).

corresponding formation of Cerin, Ain, France. A complete skeleton of *S. baumbergensis* von der Marck is known from the Upper Cretaceous of the Baumberg, Westphalia; and more fragmentary remains of *S. cranei* A. S. Woodw. occur in the English Chalk. Numerous teeth and vertebrae in the Tertiary. *S. occidentalis* Eastm., from the Maryland Miocene.

Family 9. Scylliidae.[1]

Teeth small, numerous, and pointed, several series being generally in function. Vertebrae asterospondylic, with stout radiating plates. Dorsal fins without spines, the anterior situated above or behind the pelvic fins; anal fin present; caudal fin heterocercal. Upper Jurassic to Recent.

FIG. 112.

Scyllium distans Probst. Tooth, × 2. Miocene (Molasse); Baltringen (after Probst).

Palaeoscyllium Wagner. Anterior dorsal fin opposite pelvic pair, and posterior dorsal arising in advance of anal, which is small. *P. formosum* Wagn., and *P. minus* A. S. Woodw., known by nearly complete fishes from Lithographic Stone, Bavaria.

Scyllium Cuv. (*Scylliorhinus* Blv.; *Thyellina*, *Scylliodus* Ag.) (Fig. 112). Origin of anal fin always in advance of that of posterior dorsal fin. Teeth delicate, with a high middle cusp and generally one or two small lateral denticles. Nearly complete fishes from the Upper Cretaceous of Westphalia (*S. angustum* Ag. sp.) and Mount Lebanon (*S. elongatum* Davis sp.); also numerous detached teeth from the Chalk and Tertiaries (Fig. 112). Recent.

FIG. 113.

Ginglymostoma blanckenhorni Stromer. Tooth, from the side (*a*) and from outwards (*b*), nat. size. Eocene; Egypt.

Pristiurus Bonap. As *Scyllium*, but with a series of small flat spines on each side of the upper edge of the caudal fin. *P. hassei* A. S. Woodw., a small species from the Lithographic Stone of Eichstädt, Bavaria. Recent.

Mesiteia Kramberger. Snout produced. Teeth minute and tricuspid. Anterior dorsal fin above or behind pevlic pair; anal fin much extended. Tail excessively elongated, without dermal scutes or spines. Shagreen absent or very delicate, and lateral line supported by a series of calcified rings as in Chimaeroids. *M. emiliae* Kramberger, from

[1] *Leriche, M.*, Deux Scylliidae nouveaux du Paléocène de Landana, Congo. Rev. Zool. Africaine, vol. xv., p. 398, 1927.

Upper Eocene, Monte Bolca, near Verona; *M. sahel-almae* Pict. and Humb. sp., from Upper Cretaceous, Mount Lebanon.

Cantioscyllium A. S. Woodw. Chalk; England.

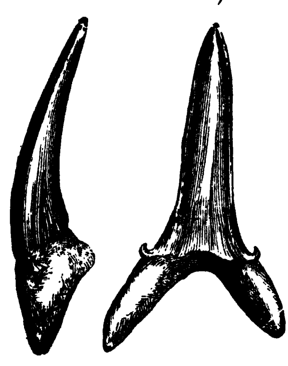
Chiloscyllium Müller and Henle, and *Ginglymostoma* Müller and Henle (*Plicodus* Winkler; *Acrodobatis* Leidy) (Fig. 113). Tertiary and Recent.

Crossorhinus Müller and Henle (*Orectolobus* Bonap.). *C. jurassicus* A. S. Woodw.[1] Upper Jurassic (Lithographic Stone); Eichstädt, Bavaria. Recent.

Family 10. **Lamnidae.**

Teeth pointed and usually large, with or without lateral denticles, the root bifurcated, and the pulp cavity completely filled with vasodentine; one series only in function at a time. Vertebral centra asterospondylic or partly tectospondylic. Dorsal fins without spines, the anterior situated opposite to the space between the pectoral and pelvic fins; anal fin present; caudal fin heterocercal. Cretaceous to Recent.

Scapanorhynchus A. S. Woodward (*Rhinognathus* Davis *nec* Fairmaire; *Mitsukurina* Jordan). Body slender, snout much elongated. Second dorsal fin small, opposed to a much extended anal fin; caudal fin much elongated, inferiorly notched near the extremity. Teeth as in *Odontaspis*. Complete skeletons of *S. lewisi* Davis sp., and *S. elongatus* A. S. Woodw., from the Upper Cretaceous of Sahel Alma, Mount Lebanon. Detached teeth (*S. rhaphiodon* Ag. sp.) in Upper Cretaceous of Europe, probably also in North America, India, Japan, Africa, and New Zealand. Small teeth (*Lamna gracilis* Ag.) from the Neocomian of France and Switzerland seem also to belong to this genus. Living in the deep sea off Japan (*Mitsukurina owstoni* Jordan).



Odontaspis cuspidata Ag. sp. Oligocene; Weinheim, near Alzey.

Odontaspis Ag. (*Triglochis* M. and H.; *Otodus* Ag. in part; *Synodontaspis*, *Parodontaspis* White, as sub-genera) (Fig. 114). Snout not much elongated. Second dorsal fin and the anal of equal size, scarcely smaller than the first dorsal. Side of tail without keel. Teeth with a slender principal cusp, with sharp lateral edges, flattened outer face, and convex inner face, also one or two pairs of small lateral denticles; root large and bifurcated. The fourth tooth (and sometimes the following one to three) from the symphysis of the upper jaw very small. Upper Cretaceous, Tertiary and Recent. *O. bronni* Ag. U. Cretaceous; Maastricht and Ciply. *O. elegans* Ag. sp., *O. macrota* Ag. sp., and *O. cuspidata* Ag. sp. (Fig. 114), from Lower Tertiaries. *O. koerti* Stromer sp., from Middle Eocene, Togoland and Nigeria.

Hypotodus Jaekel (*Jaekelotodus* Menner). Very stout teeth, but much resembling *Odontaspis*. Lower and Middle Eocene; England, France, and Belgium. Lower Eocene; Mangyschlak, Russia. Lower Oligocene; South Russia.

Lamna Cuv. (*Otodus* Ag. in part) (Figs. 115-117). Second dorsal fin and

[1] *Woodward, A. S.*, Proc. Zool. Soc., 1918, p. 231.

the anal very small. Side of tail with keel. Teeth as in *Odontaspis*, but the principal cusp usually somewhat broader and the lateral denticles larger. Vertebral centra (Fig. 117) completely asterospondylic. Very abundant in the Chalk, Tertiaries, and existing seas. Teeth of *L. appendiculata* Ag. (Fig. 115) universally distributed in Upper Cretaceous. *L. obliqua* Ag. sp. (Fig. 116), large teeth from the Eocene. *L. gafsana* White. Eocene; Tunis.

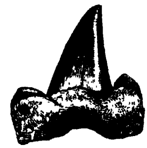


FIG. 115.
Lamna appendiculata Ag. Planer; Quedlinburg.

Oxyrhina Ag. (*Isurus* Raf.; *Anotodus* Le Hon) (Fig. 118). Only differing from *Lamna* in the teeth lacking lateral denticles. Cretaceous to Recent. *O. mantelli* Ag., the commonest Cretaceous species both in Europe and North America, the nearly complete dentition known from Kansas.[1] *O. desori* Ag., chiefly Lower Tertiary; *O. hastalis* Ag., chiefly Upper Tertiary.

Carcharoides Ameghino. Teeth resembling those of *Lamna*, but delicately serrated. Lower Tertiary (Patagonian Formation); Chubut, Argentina. Lower Tertiary (Janjukian); Geelong, Victoria, Australia.

Alopecias M. and H. Tertiary and Recent.

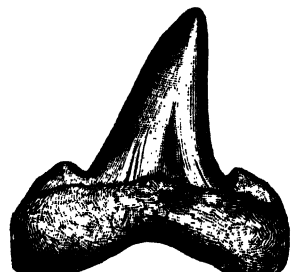


FIG. 116.
Lamna obliqua Ag. sp. External aspect of tooth. Eocene; Sheppey.

Corax Ag. (Fig. 119). Teeth low triangular, with sharp serrated edges and a large root. Vertebral centra partly tectospondylic, resembling those of *Cetorhinus*. Common in the Middle and Upper Cretaceous. *C. pristodontus* Ag., from Upper Cretaceous of Maastricht (Holland), Ciply (Belgium),

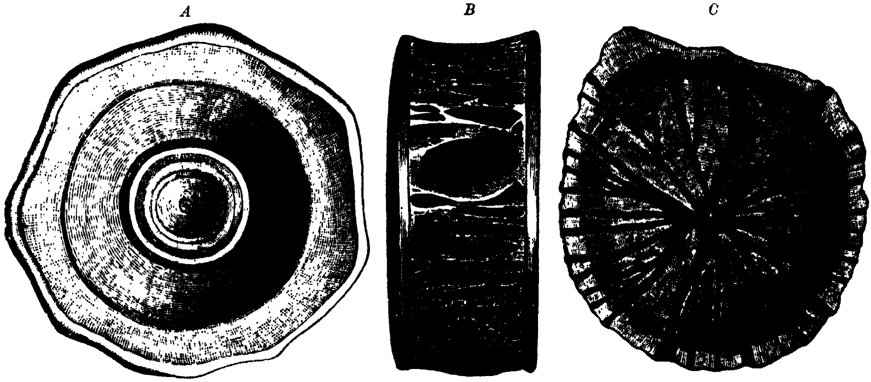


FIG. 117.
Vertebra of *Lamna*, in front (*A*) and side view (*B*), and in vertical median section (*C*). Nat. size. *A*, *B*, from Oligocene of Flonheim. *C*, from London Clay, Sheppey.

Norfolk (England), South India, North Africa (Fig. 119), and Brazil, and supposed Eocene of Alabama. *C. falcatus* Ag., European, Madagascan, and North American Cretaceous. *C. affinis* Ag. (*Pseudocorax* Priem), Upper Senonian of Europe; teeth apparently transitional to those of *Cetorhinus*.

[1] *Eastman, C. R.*, Palaeontographica, vol. xli., p. 149, 1894.

Carcharodon M. and H. (*Carcharocles* Jordan and Hannibal) (Fig. 120). Second dorsal fin and the anal very small. Side of tail with keel. Teeth very large and triangular, with serrated lateral edges, flattened outer face, convex inner face, with or without lateral denticles. Vertebral centra partly tectospondylic. One Upper Cretaceous (*C. longidens* Pillet) and one existing species (*C. rondeleti* M. and H.) which dates back to the Miocene in Europe; the others Tertiary. *C. auriculatus* Blv. Middle and Upper Eocene; Europe. *C. debrayi* Leriche. M. Eocene; France and Nigeria. *C. praemegalodon* Weiler, widely distributed in Oligocene.[1] *C. megalodon* Ag. (Fig. 120) and allied species are represented by very large teeth (up to 15 cm. deep) in the Miocene and Pliocene formations of nearly all parts of the world, in the Pleistocene of California, also on the bed of the existing oceans.

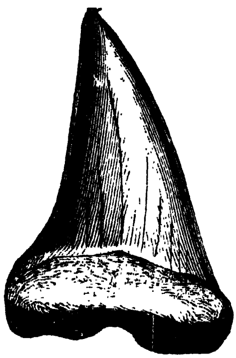


FIG. 118.
Oxyrhina plicatilis Ag. Miocene; Neudörfl, Hungary.

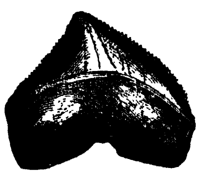


FIG. 119.
Corax pristodontus Ag. Upper Chalk; Oasis of Dachel, Libyan Desert.

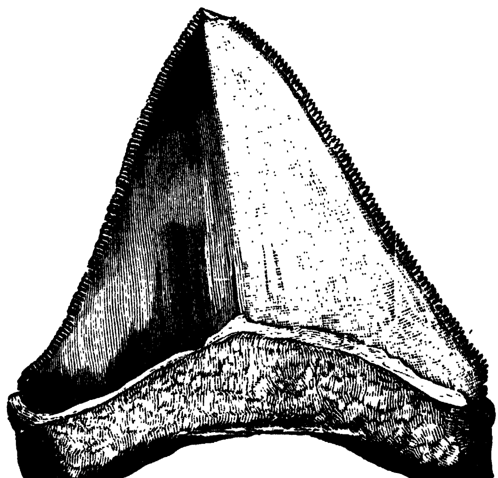


FIG. 120.
Carcharodon megalodon Ag. Miocene; Malta.

Cetorhinus Blv. (*Selache* Cuv.). Teeth very small and conical, without lateral denticles. Gill-rakers, consisting of dentine, are known from the Pliocene of Antwerp (*Hannovera aurata* Van Ben.). Claspers of male with horn-shaped spines, which have been found in the Pliocene of England and Belgium. The existing "basking shark." Allied species date back to the Oligocene in Europe.

Family 11. **Carchariidae.**

Teeth hollow, pointed and triangular, with smooth or serrated lateral borders; one series only in function at a time. Vertebral centra tectospondylic, penetrated by deep wedges of uncalcified cartilage at the bases of the neural and haemal arches. Dorsal fins without spines, the anterior situated opposite to the space between the pectoral and pelvic fins; anal fin present; caudal fin heterocercal. Tertiary to Recent.

[1] *Weiler, W.*, Notizblatt Vereins f. Erdkunde u. Hess. Geol. Landesanst. Darmstadt, 1927, p. 106.

Hemipristis Ag. (*Dirhizodon* Klunzinger) (Fig. 121). Principal teeth large, triangular and compressed, with coarsely serrated edges; anterior lower teeth slender, subulate, inwardly curved, and without denticulations, or with one or two minute points at the base. *H. serra* Ag. (Fig. 121), common in the Miocene of Europe and in the Tertiary Phosphate Beds of South Carolina and Maryland Miocene. One existing species.

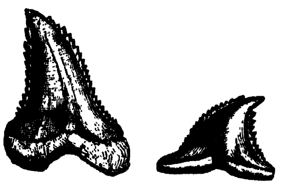


FIG. 121.

Hemipristis serra Ag. Miocene; Neudorfl, Hungary.

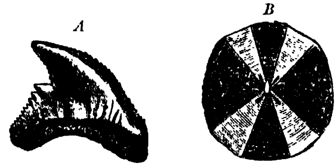


FIG. 122.

A, Tooth of *Galeocerdo aduncus* Ag. Miocene (Molasse); Pfullendorf, Baden. *B*, Section of vertebra of *Galeocerdo*. Miocene (Molasse); Baltringen (after Hasse).

FIG. 123.

Galeus affinis Probst. Miocene (Molasse); Baltringen (after Probst).

Galeocerdo Müller and Henle (Fig. 122). Teeth oblique, serrated on both margins, with a deep notch posteriorly. Eocene to Recent. *G. latidens* Ag., from the Bracklesham Beds and Middle Eocene of Belgium, Egypt, and Nigeria. *G. aduncus* Ag. (Fig. 122, *A*), a Miocene species apparently ranging to the Pliocene. *G. contortus* Gibbes, and *G. triqueter* Eastm., from the American Miocene.

FIG. 124.

A, *Carcharias* (*Aprionodon*) *frequens* Dames. Eocene; Birket-el-Qurūn, Egypt (after Dames). *B*, *Carcharias* (*Hypoprion*) *singularis* Probst. *C*, *Carcharias* (*Scoliodon*) *kraussi* Probst. *D*, *Carcharias* (*Prionodon*) *similis* Probst. Miocene (Molasse); Baltringen (after Probst).

Alopiopsis Lioy, and *Pseudogaleus* Jaekel. Nearly complete fishes from Upper Eocene, Monte Bolca, near Verona.

Galeus Cuv. (*Eugaleus* Gill; *Protogaleus* Molin) (Fig. 123). Teeth small and oblique, the margins only serrated at the base, and a deep notch posteriorly. Eocene to Recent.

Carcharias Cuv. (Fig. 124). Teeth mostly oblique and triangular, without lateral denticles, usually different in the two jaws. The lateral edges serrated to the apex (*Prionodon* Müller and Henle or *Carcharinus* Blainville) or only at the base (*Hypoprion* M. and H.), or sharp-edged but not serrated (*Scoliodon*, *Physodon* M. and H.), sometimes also erect and sharp-edged (*Aprionodon* Gill). Tertiary and Recent. *C.* (*Scoliodon*) *cuvieri* Ag. sp., represented by a nearly complete fish from Upper Eocene, Monte Bolca.

Hennigia Ihering. Teeth erect, winged at sharp-edged apex; root tripartite. *H. ungulatus* Münster sp. Miocene; Würtemberg.

Sphyrna Raf. (*Zygaena* Cuv.). Hammerhead sharks. Eocene to Recent. *S. prisca* Ag. Miocene; Europe and N. America.

Mustelus Cuv.; *Triaenodon*, *Triacis* M. and H. Recent.

B. Branchial clefts ventral. *Skates or Rays.*

Family 12. Rhinobatidae.

Trunk depressed, but elongated. Vertebrae tectospondylic. Teeth small and obtuse, hollow, several series in function. Pectoral fins large, connected with the head,

but the cartilaginous rays not reaching the end of the somewhat elongated snout. Tail robust, with two dorsals and a large caudal fin ; anal fin absent. Upper Jurassic to Recent.

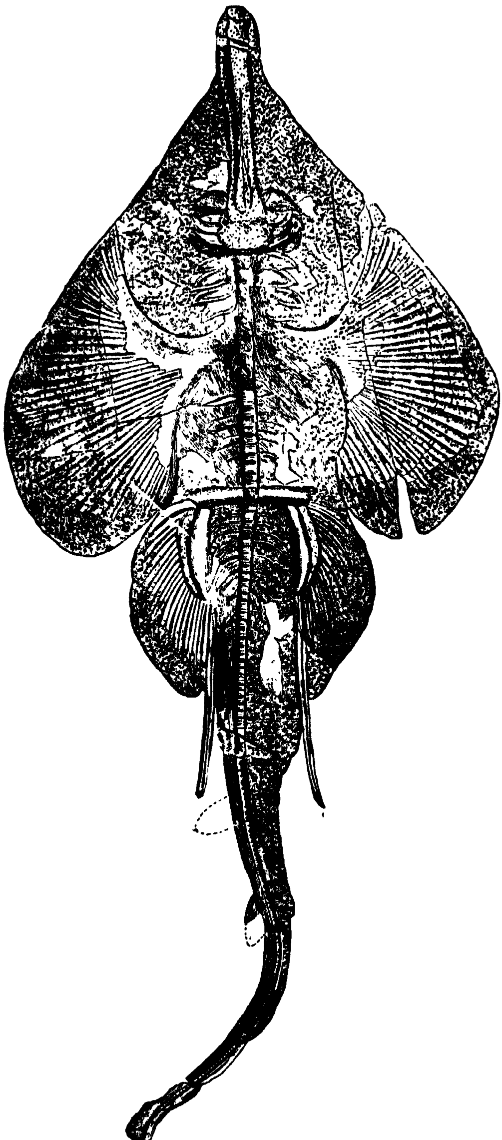


FIG. 125.

Rhinobatus mirabilis Wagn. sp. Upper Jurassic (Lithographic Stone); Eichstädt, Bavaria. (From a specimen 1·7 m. long in the Palaeontological Museum, Munich.)

Rhinobatus Bloch (*Euryarthra* Ag. ; *Spathobatis* Thioll.) (Fig. 125). Dorsal fins without spines, the anterior dorsal far behind the pelvic fins. Skin with small shagreen granules. Complete skeletons from the Lithographic Stone of Bavaria (*R. mirabilis* Wagn. sp.) and France, the Cretaceous of Mount Lebanon (*R. maronita* Pict. and Humb.) and Italy, and the Upper Eocene of Monte Bolca. Also later Tertiary and Recent.

Asterodermus Ag. Dorsal fins with small spines. Shagreen granules rather large, stellate. *A. platypterus* Ag., a small species from the Lithographic Stone of Bavaria.

Belemnobatis Thiollière. Lithographic Stone; Cerin, Ain, France. Perhaps identical with *Asterodermus*.

Rhynchobatus M. and H. Eocene to Recent. *R. vincenti* Jaekel, teeth from Middle Eocene, Belgium.

Trygonorhina M. and H. Eocene to Recent.

Family 13. **Pristidae.**[1] Saw-fishes.

Trunk elongated, slightly depressed. Vertebrae tectospondylic.

[1] *Fraas, E.*, Säge von *Propristis schweinfurthi* Dames. Neues Jahrb. f. Min., etc., 1907, vol. i., p. 1.—*Hoffmann, L.*, Neurocranium der Pristiden und Pristiophoriden. Zool. Jahrb., Abt. Anat., vol. xxxiii., p. 239, 1912.—*Stromer, E.*, Säge des Pristiden *Onchopristis numidus* Haug sp., und über die Sägen der Sägehaie. Abhandl. Bay. Akad. Wiss., vol. xxviii., no. 8, 1917.—Skelettrest des Pristiden *Onchopristis numidus* Haug sp. *Loc. cit.*, vol. xxx., no. 6, 1925.—*Vigliarolo, G.*, Monografia dei Pristis fossili. Atti R. Accad. Sci. Napoli [2], vol. iv., Append. no. 3, 1890.—*Woodward A. S.*, The Cretaceous Saw-fish *Sclerorhynchus atavus*. Geol. Mag., 1892, p. 529.

Teeth of the mouth minute and obtuse, several series in function. Pectoral fins rather large, united with the head, but not extended to the long, depressed, sword-like rostrum, which is strengthened with lateral cartilages, and armed with a row of large dermal teeth on each lateral border. Upper Cretaceous to Recent.

Sclerorhynchus A. S. Woodw. Teeth of rostrum comparatively small, enamelled at apex, and not fixed in sockets. Rostrum thus resembles that of *Pristiophorus*, but differs from the latter and agrees with *Pristis* in the great development of a pair of lateral cartilages. *S. atavus* A. S. Woodw. and *S.*

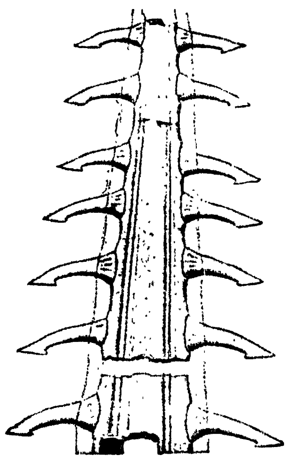


FIG. 126.

Onchopristis numidus Haug sp. Portion of rostrum, restored by Stromer. Cenomanian; Egypt. $^1/_4$ nat. size.

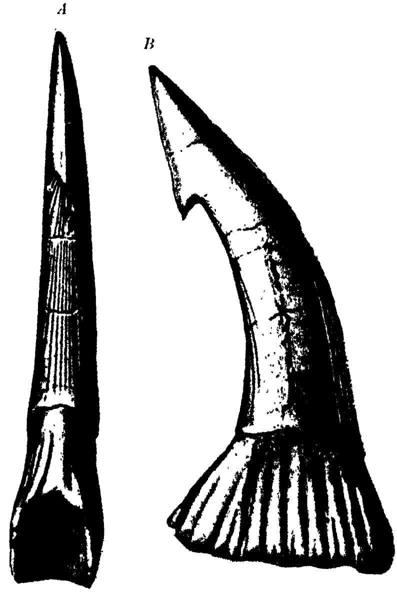


FIG. 127.

Onchopristis numidus Haug sp. Rostral tooth, from behind (*A*) and from the side (*B*). Cenomanian; Egypt. Nat. size, after Stromer.

hiram Hay, known by nearly complete skeletons less than a metre in length from Upper Cretaceous, Mount Lebanon.

Onchosaurus Gervais (*Titanichthys, Gigantichthys* Dames). Rostral teeth large, not fixed in sockets; enamelled only at the short barbed apex. *O. pharao* Dames sp. Upper Cretaceous; Egypt. Also France.

Schizorhiza Weiler. Small rostral teeth enamelled, deeply cleft at base to clasp edge of rostrum. Upper Cretaceous (Nubian Sandstone and Phosphates); Egypt.

Ischyrhiza Leidy. *I. mira* Leidy. Upper Cretaceous; New Jersey and Maryland, U.S.A., and Chile.

Onchopristis Stromer (Figs. 126, 127). Rostrum slender and much elongated; rostral teeth also slender, not fixed in sockets, in about twelve well-spaced pairs, each tooth barbed at the apex and enamelled nearly to the base. *O. numidus* Haug sp. Upper Cretaceous (Cenomanian); North Africa.

Propristis Dames (*Amblypristis* Dames; *Eopristis* Stromer) (Fig. 128).

Rostral teeth as in *Pristis*, but shorter and broader, and not implanted in cartilage. Middle Eocene; Birket-el-Qurūn, Egypt, and Ameki, S. Nigeria.

Pristis Latham (*Oxypristis* Hoffm.). Teeth of rostrum peg-like, firmly implanted in sockets of calcified cartilage. Eocene to Recent.

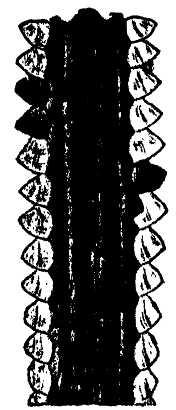


Fig. 128.
Propristis schweinfurthi Dames. Distal end of rostrum. Eocene; Egypt. 1/4 nat. size (after E. Fraas).

Family 14. **Rajidae.**

Trunk much depressed, forming a broad, usually rhombic disk with the pectoral fins, which extend from the snout to the pelvic fins. The latter fins with a strong, unsegmented, cartilaginous ray in front. Teeth small, with bifurcated root and rhombic crown, forming a close pavement in each jaw. Tail very slender, without spines, and the caudal fin small or absent; anal fin absent. Skin with small, pointed shagreen granules and larger, scattered, spinous, placoid tubercles. Upper Cretaceous to Recent.

Cyclobatis Egerton. Disk circular or oval, and tail very short, without median fins. Rays of paired fins few and well spaced, the pectorals united in front of the head. Pelvic arch with very large pre-pubic processes. *C. oligodactylus* Egerton, from Upper Cretaceous, Hakel and Hajoula, Mount Lebanon.

Raja Cuv. (*Actinobatis* Ag.) (Fig. 2, p. 4). Teeth pointed in male, blunt in female. Upper Cretaceous, Mount Lebanon (*R. expansa* Davis sp.) to Recent. Dermal tubercles of existing *R. clavata* Linn. (*R. antiqua* Ag.), in Pliocene Crags of Norfolk and Suffolk.

Platyrhina M. and H. Upper Eocene (Monte Bolca) to Recent.

Family 15. **Torpedinidae.** Torpedoes.

Trunk much depressed, forming a broad and rounded disk with the pectoral fins which do not extend forwards to the broadly rounded anterior end of the head. Tail short and fleshy, with well-developed dorsal and caudal fins; anal fin absent. Skin naked. An electric organ between the pectoral fins and the head. Eocene to Recent.

Torpedo Duméril (*Narcobatis* Blv.). Sometimes supposed to be represented by skeletons in Upper Eocene of Monte Bolca, but doubtful. Teeth of *T. hilgendorfi* Jaekel from Upper Tertiary, Balangi, Cameroon. Recent.

Narcine Henle. Upper Eocene of Monte Bolca (*N. molini* Jaekel) and Recent.

Family 16. **Trygonidae.** Sting-rays.

Trunk much depressed, forming a disk with the very broad pectoral fins, which meet in front of the snout, and constitute the anterior border of the head. Teeth small, rhombic or polygonal, with bifurcated root, and forming a close pavement. Tail very slender, sharply separated from the disk, the dorsal fins usually replaced by several stout imbricating spines of vasodentine, which are antero-posteriorly compressed and armed with a row of recurved hooklets on each lateral border; anal fin absent. Skin naked, with large conical plates of vasodentine, sometimes fused into groups, usually raised into a short spine. Cretaceous to Recent.

Trygon Adanson (*Trygonobatus* Blv.; *Alexandrinum* Molin) (Figs. 129, 130). Tail elongated, with long, flattened dorsal spines. Dermal plates of very variable form and size. *T. gazolae* Ag.; *T.* (*Alexandrinum*) *molini* Zigno; *T. zignoi* Molin, known by nearly complete skeletons from the Upper Eocene of Monte Bolca.[1] Isolated dermal plates (Fig. 130) have been described as referable to *Raja*, *Acipenser*, *Dynatobatis* Larrazet, and *Acanthobatis* Larr.

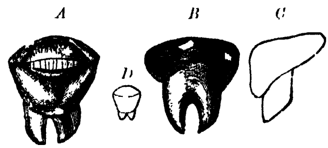


FIG. 129.

Trygon rugosus Probst. Tooth, anterior (*A*), posterior (*B*), and lateral (*C*) aspects, enlarged, and the same nat. size (*D*). Miocene (Molasse); Baltringen (after Probst).

Taeniura, *Urolophus* M. and H. Upper Eocene (Monte Bolca and Monte Postale) and Recent.

Xiphotrygon Cope (*Heliobatis* Marsh). Resembling *Trygon*, but teeth cuspidate. *X. acutidens* Cope, known by complete skeletons from Eocene Green River Shales of Wyoming.

Oncobatis Leidy. Dermal tubercles. Pliocene; Idaho.

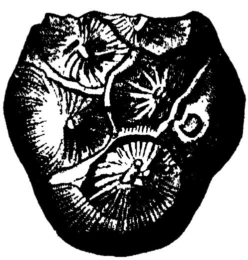


FIG. 130.

Trygon (*Acanthobatis*) *tuberculosus* Probst sp. Dermal tubercle, nat. size. Miocene (Molasse); Baltringen.

Rhombodus Dames.[2] Crushing teeth and caudal spines from Upper Cretaceous, Maastricht, Holland. Teeth also from Senonian Phosphates of Egypt, and the Quiriquina Formation of Chile.

Myledaphus Cope. Teeth. Upper Cretaceous; Montana, Wyoming, and New Mexico, U.S.A., and Alberta, Canada.

Ptychotrygon Jaekel. Transversely ridged enamelled teeth. *P. triangularis* Reuss sp. Upper Cretaceous; Bohemia.

Hypolophus M. and H. Teeth in Lower Eocene. Recent.

Hypolophites Stromer.[3] Flat hexagonal or rhombic teeth forming a close pavement; a median row of teeth in one jaw, none in the other jaw. Lower Eocene; Togoland, Nigeria, and Congo Free State.

? *Parapalaeobates* Weiler. Crushing teeth with coarsely reticulated crushing surface; consisting of dentine of which the fine tubules radiate from one small centre. Upper Cretaceous (Nubian Sandstone and Phosphates); Egypt.

Family 17. **Ptychodontidae.**

Trunk probably not much depressed. Quadrangular crushing teeth with thick enamel (ganodentine), which is variously ridged and rugose; attached surface of root not grooved. Teeth arranged on symphysis of jaws in several longitudinal series, one median, the others symmetrically paired. Vertebrae tectospondylic. Cretaceous.

Hylaeobatis A. S. Woodw. Teeth solid, irregularly ridged, transversely elongated. Wealden; England.

[1] *Eastman, C. R.*, Mem. Carnegie Mus., vol. vi., no. 5, p. 316, 1914.
[2] *Umbgrove, J. H. F.*, Leidsche Geol. Mededeel., vol. ii, p. 15, 1926.
[3] *Stromer, E.*, Monatsb. Deutsch. Geol. Ges., vol. lxii., p. 490, 1910.—*Leriche, M.*, Ann. Mus. Congo Belge—Géol., Paléont., Sér. iii., vol. i., p. 71, 1913.

Ptychodus Ag.[1] (*Aulodus* Dixon; *Hemiptychodus* Jaekel) (Figs. 131-134). Known only by the dentition and vertebrae. Teeth solid, with a raised

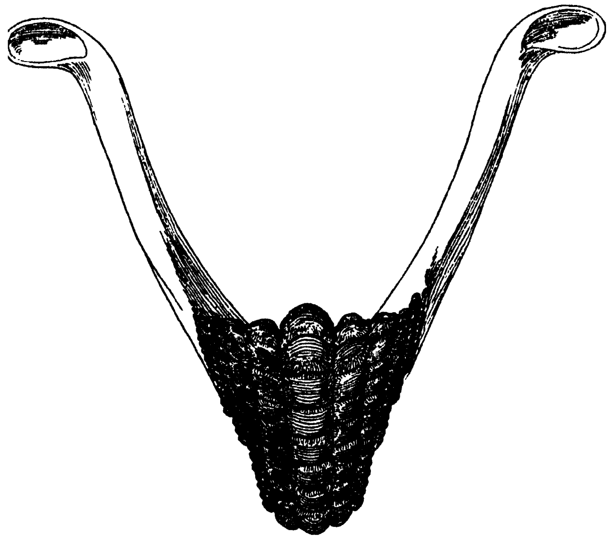


FIG. 131.
Ptychodus decurrens Ag. Lower jaw. Lower Chalk; England. 2/3 nat. size (after A. S. Woodward).

crown, which is transversely or radially ribbed, and sharply separated by a constriction from the smaller, smooth root. They are arranged in thirteen

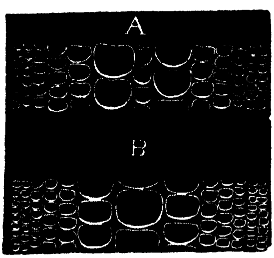


FIG. 132.
Ptychodus decurrens Ag. Diagram of arrangement of teeth in upper (*A*) and lower (*B*) jaws, much reduced. Lower Chalk; England (after A. S. Woodward).

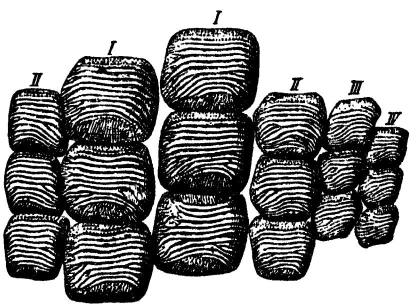


FIG. 133.
Ptychodus decurrens Ag. Teeth of four inner paired rows of upper jaw. Lower Chalk; England. 1/2 nat. size (after A. S. Woodward).

to nineteen antero-posterior series (Figs. 131-133). In one jaw, presumably lower, the median series of teeth is the largest, and the lateral rows are disposed symmetrically, diminishing in size outwards. In the opposing jaw the median series is very small, and the first lateral row on each side large, with

[1] *Canavari, M.*, Un notevole esemplare di *Ptychodus* Agassiz. Palaeont. Ital., vol. xxii., p. 35, 1916.—*Dibley, G. E.*, Teeth of *Ptychodus* and their Distribution in the English Chalk. Quart. Journ. Geol. Soc., vol. lxvii., p. 263, 1911.—*Woodward, A. S.*, Jaws of *Ptychodus* from the Chalk. Quart. Journ. Geol. Soc., vol. lx., p. 133, 1904.

the outer lateral series diminishing. Common in the Upper Cretaceous of Europe and North America. Also found in Syria and Japan, and in an Upper Cretaceous deep-sea deposit in the Island of Timor.[1]

Heteroptychodus Yabe and Obata. Teeth as in *Ptychodus*, but without definite marginal area. Cretaceous; Japan.

FIG. 134.
Ptychodus polygyrus Ag. Tooth, oral and posterior views, nat. size. Greensand; Regensburg.

Family 18. **Myliobatidae.**
Eagle-rays.

Trunk much depressed, forming a broad disk with the very large pectoral fins, which are interrupted at the sides of the head, but reappear as one or a pair of small cephalic fins at the extremity of the snout. Teeth rather large, forming a close pavement in both jaws; lower face of root marked with straight antero-posterior furrows. Skin naked. Tail very slender, with one or several flattened spines behind the single dorsal fin; anal fin absent. Cretaceous to Recent.

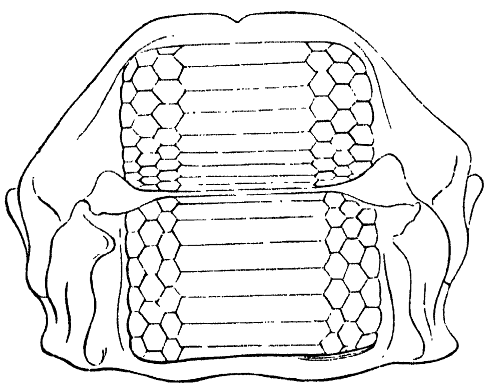


FIG. 135.
Jaws of *Myliobatis aquila* Cuv. Anterior aspect. Recent; Mediterranean (after Agassiz).

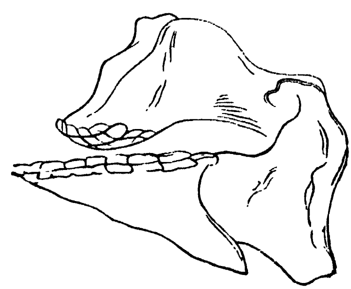


FIG. 136.
Jaws of recent *Myliobatis*, lateral aspect.

Most of the surviving genera of this family are represented in the Tertiary by isolated teeth and spines, or by the complete dentition.

Apocopodon Cope.[2] Teeth quadrate or sexangular, mostly broader than long, their nearly flat oral surface marked with antero-posterior wrinkles; attached surface of root with few widely spaced antero-posterior furrows. *A. sericeus* Cope, from Upper Cretaceous, Pernambuco, Brazil.

Promyliobatis Jaekel. A skeleton from the Upper Eocene of Monte Bolca, apparently showing pectoral fins less completely interrupted at side of head than in recent *Myliobatis*, otherwise resembling the latter. *P. gazolae* Zigno sp.

[1] *Beaufort, L. F. de*, 2e Nederland. Timor-Expeditie. Jaarb. Mijnwesen Ned. O.-Indie Verhand., iv, p. 61, 1920 (1923). Also *Weiler, W.*, Neues Jahrb. f. Min., etc., Beil.-Bd. 67, Abt. B, p. 293, 1932.

[2] *Woodward, A. S.*, Geol. Mag., 1907, p. 194.

Myliobatis Cuvier (*Pastinaca* Gronow) (Figs. 135-138).[1] The dental pavement of the jaws consists of seven antero-posterior rows of sexangular flattened teeth pressed together. The lower dentition is longer and less arched than that of the upper jaw (Fig. 136). In young examples all the teeth are similar in form and size, but during growth the median series rapidly increases in width, and eventually becomes from three to eight times as broad as long, while the shape of the lateral series remains unchanged.[2] The strongly developed root of each tooth is marked with several parallel grooves on its lower and lateral faces. Numerous species represented by the dentition in the Tertiaries, and caudal spines also known (Fig. 138). *M. dixoni* Ag.; *M. striatus* Buckl.; *M. toliapicus* Ag. (Fig. 137) from English Eocene. *M. pentoni* A. S. Woodw., the largest known species, with lower dentition 16 cm. wide, from Eocene, Mokattam Hills, Cairo. *M. magister* Leidy, the largest American species, known by complete dentition from the South Carolina Eocene.

FIG. 137.
Myliobatis toliapicus Ag. Imperfect dentition. Middle Eocene; Bracklesham, Sussex.

Rhinoptera Müller (*Zygobates* Ag.; *Mylorhina* Gill). Dentition of both jaws strongly arched antero-posteriorly. Teeth flattened and sexangular, in five to nine antero-posterior rows, and mostly broader than long, but diminishing in breadth outwards. Cretaceous to Recent. *R. prisca* A. S. Woodw., from Upper Cretaceous, Pernambuco, Brazil. *R. daviesi* A. S. Woodw., from London Clay, Sheppey and Belgium. *R. sherborni* White, from Middle Eocene, Nigeria.

Aetobatis M. and H. (*Goniobatis* Le Hon; *Stoasodon* Cantor). Teeth very broad, in a single antero-posterior series. Tertiary and Recent; wide distribution.

Typical egg-capsules of skates occur in the Oligocene of Switzerland.[3]

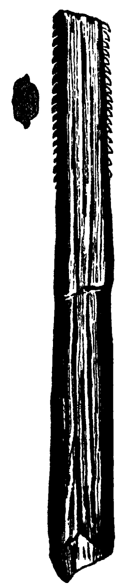


FIG. 138.
Myliobatis serratus H. von Meyer. Caudal spine. Oligocene; Weinheim, near Alzey.

Sub-Order 2. BRADYODONTI.

Teeth few during lifetime, in slow succession. Placoid scales often fused into plates.

These are Palaeozoic Selachians in which the teeth are largely composed of tubular dentine (*palodentine* of Jaekel), resembling that in the tritors of the dental plates of Chimaeroids.

[1] *Salinas, E.*, Sopra alcuni Myliobatidi fossili della Sicilia. Giorn. Sci. Nat. ed Econom. Palermo, vol. xx., p. 1, 1900.

[2] *Stromer, E.*, Zeitschr. Deutsch. Geol. Ges., vol. lvi., p. 249, 1904; also Monatsb., p. 203.—*Woodward, A. S.*, Ann. Mag. Nat. Hist. [6], vol. i., p. 36, 1888.

[3] *Peyer, B.*, Rochen-Eikapseln aus den Horwerschichten (unteres Stampien) von Grisigen, Kt. Luzern. Eclogae geol. Helvet, vol. xxi., p. 407, 1928.

Family 1. **Cochliodontidae.**

Teeth tumid or flattened for crushing, and not more than six or seven in succession in each row; one or two rows on each ramus of the jaw usually fused into continuous plates, which curve into a little scroll at the outer border; not more than one or two paired rows of teeth between these plates and the symphysis. Paired spines often present on the head. Upper Devonian, Carboniferous and Permian.

Our knowledge of this remarkable Upper Palaeozoic family is still very incomplete. Of two genera (*Helodus* and *Menaspis*) the impression of the trunk is known; of all the others only teeth or fin spines and, very rarely, complete jaws occur. According to Jaekel, the genera here included represent more than one family. He refers *Cochliodus*, *Deltoptychius*, *Menaspis*, etc., to a

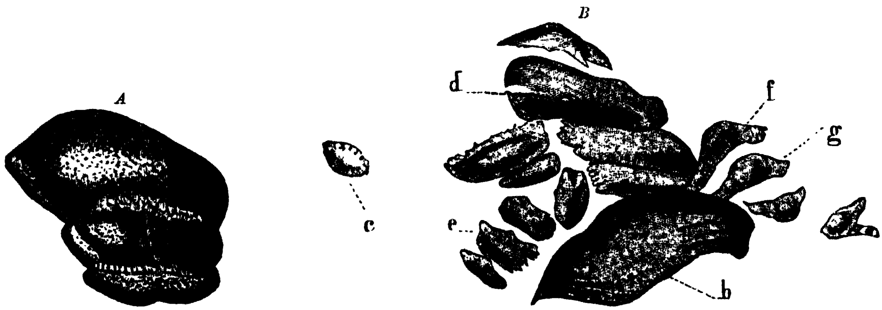


FIG. 139.

Psephodus magnus Ag. *A*, Three teeth in connected series, nat. size, from the Carboniferous Limestone of Armagh (after Davis). *B*, Associated upper teeth from remains of head found in Calciferous Sandstones, East Kilbride, Lanarkshire. *b*, large tooth somewhat broken; *c*, small tooth identical with *Helodus rudis* M'Coy; *d*, slender teeth identical with *Helodus planus* Ag.; *e*, Helodont teeth; *f*, *g*, teeth identical with *Lophodus didymus* and *L. laevissimus* Ag. sp. Nat. size (after Traquair).

Sub-Order *Trachyacanthi* of the Order *Holocephali*, while he places *Psephodus* with the *Petalodontidae* and *Edestidae* in the Sub-Order *Statodonti* of the Order *Selachii*.

Helodus Ag. Teeth elongated, with a raised tumid centre; in not more than six rows on each ramus of the jaw, all closely similar and none completely fused into a plate. Anterior dorsal fin with a laterally compressed, broad, smooth spine. *H. simplex* Ag., English, French, and Belgian Coal Measures. Teeth in Upper Devonian, Missouri, U.S.A.

Pleuroplax A. S. Woodw. (*Pleurodus* Hancock and Atthey, *nec* Wood, *nec* Harlan).[1] Dental plates with feeble transverse ridges, and the antero- and postero-lateral borders indented between these ridges. These teeth sometimes associated with others of the *Helodus*-type. Anterior dorsal fin with spine as in *Helodus*. *P. rankinei* H. and A., from English, French, and Belgian Coal Measures. Other species from Upper and Lower Carboniferous of Europe and North America.

Psephodus Ag.[2] (Fig. 139). Teeth of one row in each ramus of jaw fused into a rhombic or rhomboidal dental plate, which is convex and gently arched, with crenulated border. Other separate teeth numerous, of the forms known

[1] *Davis, J. W.*, Ann. Mag. Nat. Hist. [6], vol. v., p. 291, 1890.
[2] *Traquair, R. H.*, Trans. Geol. Soc. Glasgow, vol. vii., p. 392, 1885.

under the names of *Helodus*, *Lophodus*, *Rhamphodus*, and *Aspidodus*. Carboniferous Limestone; Europe, India, and North America.

Sandalodus Newberry and Worthen (*Trigonodus*, *Vaticinodus* N. and W.; *Orthopleurodus* St. John and Worthen). Supposed upper dental plates triangular, thick, slightly inrolled. Supposed lower dental plates more strongly inrolled. *S. morrisi* Davis. Carboniferous; Ireland, England, Belgium, and North America.

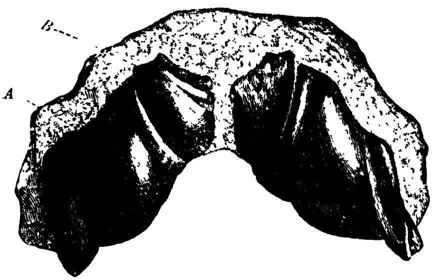


FIG. 140.
Cochliodus contortus Ag. Dentition, $^3/_4$ nat. size. Carboniferous Limestone; Armagh. *A*, large posterior dental plate; *B*, small dental plate; anterior teeth wanting.

Cochliodus Ag. (Fig. 140). Two rows of teeth on each ramus of each jaw fused into strongly arched dental plates, the posterior one very large, with a broad median area bounded in front and behind by an oblique furrow, the anterior plate comparatively small, rhomboidal in shape. Symphysial series of *C. latus* Leidy, from Keokuk Limestone of Mississippi Valley, the largest known species, originally described as *Helodus coxanus* Newb. *C. contortus* Ag. (Fig. 140), from Carboniferous Limestone; Ireland, England, Belgium, and North America.

Streblodus Ag. As *Cochliodus*, but hinder dental plate with two to three broad oblique folds. *S. oblongus* Ag., and *S. colei* Davis, from Carboniferous Limestone, Armagh. Other species from England, Belgium, and North America.

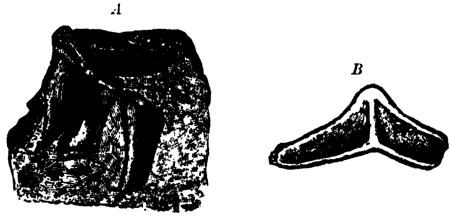


FIG. 141.
Menaspis armata Ewald (*Chalcodus permianus* Zittel). Dentition from above (*A*), and below, attached surface (*B*), nat. size. Kupferschiefer; Glücksbrunn, Thuringia.

Deltoptychius Ag.[1] Two rows of teeth in each ramus of each jaw fused into a single triangular plate without transverse ridges or furrows. Head with pair of spines of form named *Oracanthus* Ag. *D. acutus* M'Coy. sp. Carboniferous Limestone; British Isles. Other species in Belgium and North America.

Tomodus, *Cyrtonodus* Davis; *Chitonodus* St. John and Worthen; *Poecilodus* Ag.; *Deltodus* Ag. (*Taeniodus* St. J. and W.); *Xystrodus* Ag. (*Platyxystrodus* Hay). Carboniferous Limestone; Europe and North America.

Menaspis Ewald, emend. Jaekel[2] (*Dichelodus* Giebel; *Chalcodus* Zittel) (Figs. 141, 142). Head and back covered with longitudinal series of tuberculated or spiny, partially keeled placoid scales and small shagreen granules. On each side of the front portion of the head a triangular spine, provided with a broad, hollow base and covered with tubercles of ganodentine. Further back on each side three smooth, thin, arched spines fixed by a conspicuous basal process in the skin of the head, curved inwards, and apparently consisting of vaso-

[1] *Woodward, A. S.*, Quart. Journ. Geol. Soc., vol. lxxi., p. lxviii, 1915.
[2] *Dean, B.*, The Permian Fish *Menaspis*. Amer. Geologist, vol. xxxiv., p. 49, 1904.—*Jaekel, O.*, Über *Menaspis*. Sitzungsb. Ges. naturf. Freunde, Berlin, 1891, p. 115.—*Reis, O.*, Über die Kopfstacheln von *Menaspis armata*. Geogn. Jahreshefte, Munich, 1891.—*Weigelt, J.*, Leopoldina (Halle), vol. vi., p. 606, 1930.

dentine; the middle pair of these spines more than twice as long as the others. Dentition consisting of one pair of Cochliodont teeth in each jaw (Fig. 141). *M. armata* Ewald, from U. Permian (Kupferschiefer) of Germany.

Family 2. **Petalodontidae.**[1]

Teeth antero-posteriorly compressed, transversely elongated, closely arranged in longitudinal and transverse rows. Crown enamelled, more or less bent backwards, either with a sharp cutting edge or very obtuse, the anterior face convex, the posterior face concave; root deep, separated from the crown by a constriction, usually with enamel folds immediately above it. Carboniferous and Permian.

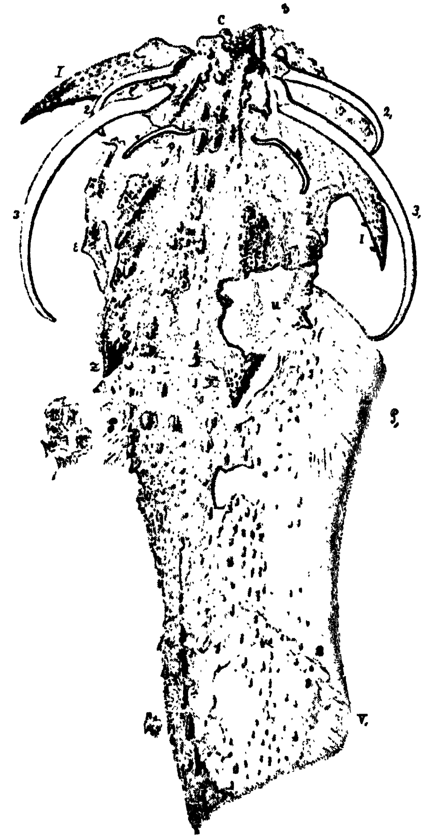


FIG. 142.

Menaspis armata Ewald. Imperfect head and trunk. Kupferschiefer; Thuringia. *P*, pectoral fins; *V*, pelvic fins; *Z*, conical dermal scutes; *1-4*, paired head spines. $^2/_3$ nat. size (after Jaekel).

In most genera of this family several successional rows of teeth are functional in the mouth at one time; but in the highly specialised genera *Petalorhynchus* and *Janassa* (perhaps also *Glossodus*) only one row is functional, the preceding teeth being thrust downwards and backwards to serve as supports. In *Janassa* and *Ctenoptychius* the trunk is depressed, with relatively large pectoral fins. Dermal spines have been found only in *Polyrhizodus*.

Petalodus Owen (*Chomatodus* Ag. in part; *Sicarius* Leidy; *Antliodus* Newb.; *Lisgodus* St. John and Worthen) (Fig. 143). Teeth much antero-posteriorly compressed and transversely elongated. Crown leaf-shaped, with cutting edge, and sharp basal margin with enamel folds; root long and comparatively slender, truncated below. *P. acuminatus* Ag. sp., and other species from the Carboniferous Limestone of England, Scotland, Ireland, Belgium, Russia, and North America. Rare in the Coal Measures of North America.

Ctenopetalus Davis (*Harpacodus* Davis; *Serratodus* de Koninck; *Peripristis* St. John and Worth.). As *Petalodus*, but edge of tooth serrated or crimped. Carboniferous Limestone; Europe and North America.

Petalorhynchus Newb. and Worth. Teeth much antero-posteriorly compressed and acuminate, with undivided root. Each functional tooth supported

[1] *Jaekel, O.*, Über die Organisation der Petalodonten. Zeitschr. Deutsch. Geol. Ges., vol. li., p. 259, 1899.—*Woodward, A. S.*, Dentition of the Petalodont Shark, *Climaxodus*. Quart. Journ. Geol. Soc., vol. lxxv., p. 1, 1919. See also *Weigelt, J.*, Leopoldina (Halle), vol. vi., p. 604, 1930.

by its predecessors, which are fused together. Carboniferous Limestone; Europe and North America.

Fissodus St. John and Worthen. Carboniferous; North America and Scotland.

Glossodus M'Coy; *Mesolophodus* A. S. Woodw. Carboniferous Limestone; Ireland.

Polyrhizodus M'Coy (*Dactylodus* Newb.) (Fig. 144). Teeth robust, with a

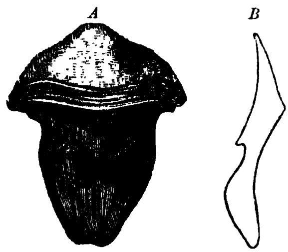


FIG. 143.
Petalodus alleghaniensis Leidy. Tooth in front view (*A*) and transverse section (*B*), 1/2 nat. size. Coal Measures; Springfield, Illinois (after Newberry).

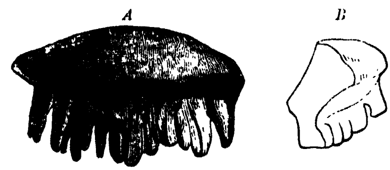


FIG. 144.
Polyrhizodus magnus M'Coy. Tooth in front view (*A*) and transverse section (*B*), 1/2 nat. size. Carboniferous Limestone; Armagh (after M'Coy).

tumid crown tapering to a transverse cutting edge, and the root much subdivided. *P. magnus* M'Coy, and other species from the Carboniferous Limestone of Ireland, England, Russia, and North America. With *P. rossicus*

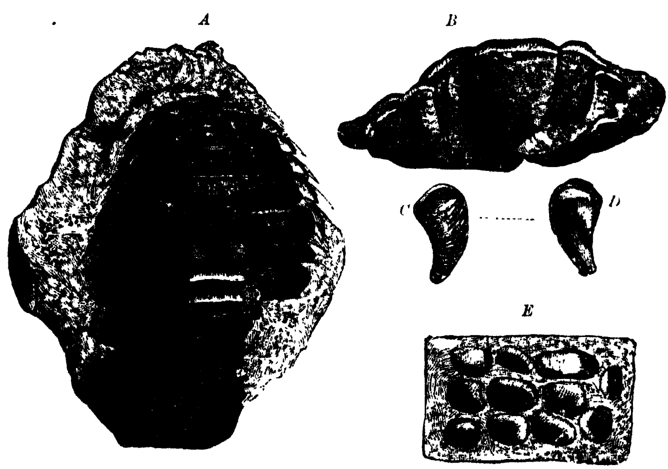


FIG. 145.
Janassa bituminosa Schloth. sp. Kupferschiefer; Glücksbrunn, Thuringia. *A*, Upper and lower dentition. *B*, Cross-section, anterior view of teeth. *C*, Tooth from behind, and *D*, from in front. Nat. size. *E*, Dermal tubercles, enlarged.

Inostr. in the Carboniferous Limestone of Russia are found tuberculated dermal spines which curve forwards like *Physonemus* M'Coy.

Ctenoptychius Ag. (*Petalodopsis* Davis). Teeth antero-posteriorly compressed, with sharp coarsely serrated edge. Shagreen strongly marked with

transverse flutings. *C. apicalis* Ag. with depressed trunk and relatively large pectoral fins. English Coal Measures.

Pristodus Davis. Lower Carboniferous; Great Britain.

Climaxodus M'Coy. Teeth as in *Petalodus*, but stouter and blunter, sometimes without rugae at the base of the crown; arranged in five to seven antero-posterior rows, of which three to five are high-crowned and on the

FIG. 146.

Janassa bituminosa Schloth. sp. Head and pectoral region. Kupferschiefer; Thuringia. *L*, labial cartilage; *Mz*, middle row of upper dentition; *Ppt*, propterygium of pectoral fin; *Uk*, lower jaw; *Ukg*, lower dentition. 2/3 nat. size (after Jaekel).

jaw symphysis, and the lateral paired row is low-crowned, extending backwards along the rami. All the teeth in function in the mouth at one time, eventually nine or ten transverse rows. *C. imbricatus* M'Coy. Carboniferous Limestone; England. *C. wisei* Traq. sp. Calciferous Sandstone; Lanarkshire, Scotland. *C. linguaeformis* Atthey. English and Scottish Coal Measures.

Janassa Münster (*Dictaea*, *Byzenos* Münster) (Figs. 145-148). Teeth with obtuse cutting edge much reflexed, and the numerous enamel folds at the base of the posterior face forming prominent transverse ridges; root long and slender, undivided. These teeth arranged in five to seven antero-posterior rows, and from seven to ten transverse (successional) rows; a single transverse row in function at one time, supported by the previous successive transverse rows which are thrust downwards and backwards beneath them (Fig. 147). Pectoral fins very large, reaching as far forwards as the head; a space between these and the pelvic fins, which are relatively small. Skin covered with oval

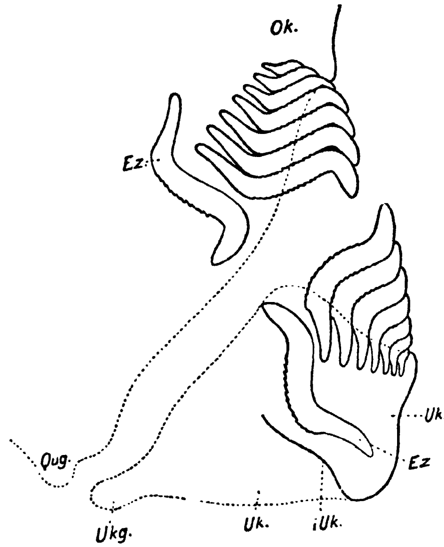


FIG. 147.

Janassa bituminosa Schloth. sp. Vertical section antero-posteriorly across jaws, reconstructed by Jaekel. *Ez*, successional teeth not yet erupted ; *Ok*, upper jaw ; *Qug*, articular end of upper jaw ; *Uk*, lower jaw ; *Ukg*, articular end of lower jaw.

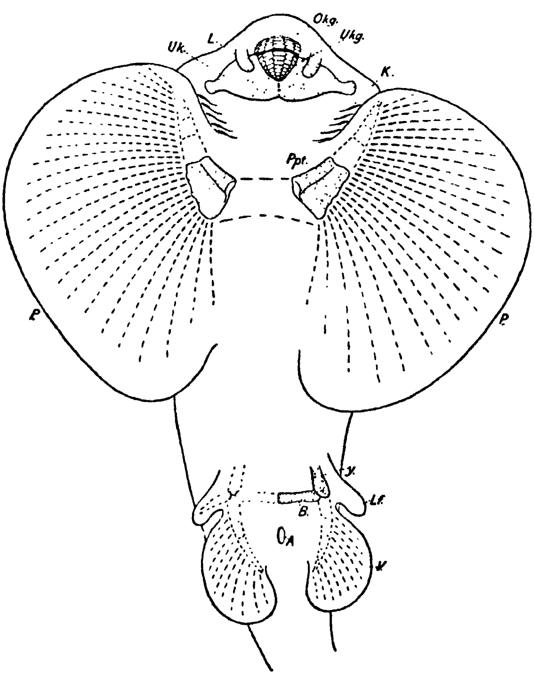


FIG. 148.

Janassa bituminosa Schloth. sp. Restoration by Jaekel, about $^1/_4$ nat. size. *A*, cloacal opening ; *B*, pelvis ; *K*, gill-clefts ; *L*, labial cartilage ; *Lf*, separate anterior part of pelvic fin ; *Okg*, upper dentition ; *P*, pectoral fin ; *Ppt*, part of propterygium ; *Uk*, lower jaw ; *Ukg*, lower dentition ; *V*, pelvic fin ; *y*, perhaps iliac process of pelvis.

or quadrate, smooth shagreen granules. *J. bituminosa* Schloth. sp. (Figs. 145-148), represented by important specimens from the Permian Kupferschiefer of Hesse and Thuringia, also from the Marl Slate of Durham. Teeth of *J. strigilina* Cope, from the Permian of Illinois, U.S.A.

Fig. 149. *Callopristodus pectinatus* Ag. sp. Lower Carboniferous; Scotland. Nat. size.

? *Callopristodus* Traquair (Fig. 149). Crown low and crimped, root subdivided. *C. pectinatus* Ag. sp., from the Coal Measures of England and Lower Carboniferous of Scotland, also from Coal Measures of Nova Scotia.

Family 3. **Psammodontidae.**

Known only by flat or slightly arched quadrilateral teeth, with punctate or finely rugose grinding surface, arranged in two longitudinal series. Root of tooth not extending beyond the crown, its lower face parallel with oral face of crown. Carboniferous.

Psammodus Ag. (*Archaeobatis* Newberry; *Homalodus*, *Astrabodus* Davis) (Fig. 150). Teeth quadrangular, with relatively thick base, smooth or feebly striated on the attached surface. The paired series not bilaterally symmetrical. *P. rugosus* Ag. (Fig. 150), from Carboniferous Limestone of Ireland, Scotland, England, Wales, and Belgium. Allied species in Russia and North America. Largest tooth of *P. gigas* Newb. sp., from Lower Carboniferous, Indiana, measuring 15 cm. across.

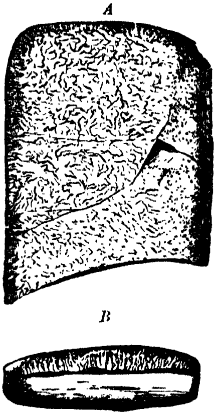


Fig. 150. *Psammodus rugosus* Ag. Imperfect tooth from above (*A*) and in transverse section (*B*), nat. size. Carboniferous Limestone; Armagh. Nat. size.

Lagarodus Jaekel. *L. angustus* Trautschold sp. Upper Carboniferous; Mjatschkowa, Moscow. Other species in Coal Measures, North Staffordshire, and Carboniferous Limestone, Bristol.

Family 4. **Copodontidae.**

Known only by flat or slightly arched quadrilateral teeth, which are bilaterally symmetrical; apparently a single tooth, or with a second tooth just behind, on the symphysis of the jaw; root at least in part extending laterally beyond the crown, its attached face nearly smooth and parallel with that of the crown. Upper Devonian and Carboniferous.

Copodus Davis (*Mesogomphus*, *Rhymodus*, *Characodus*, *Pinacodus* Davis). Comparatively small median teeth, narrower in front than behind, divided into two unequal parts by a transverse suture. *C. cornutus* Davis and allied species from Lower Carboniferous of Ireland, England, Belgium, and North America.

Labodus Davis. Lower Carboniferous; Ireland, England, and North America.

Solenodus Trautschold. Upper Carboniferous; Mjatschkowa, Moscow.

Acmoniodus Hussakof and Bryant. Two Copodont teeth, one behind the other, fused together into a pentagonal plate by the great extension of the root. *A. clarkei* Huss. and Bry., from Upper Devonian, Erie Co., New York, U.S.A., with dental plate about 12 cm. across.

Order 7. HOLOCEPHALI. Chimaeras.[1]

Pterygoquadrate arcade completely and immovably fused with the cranium (autostylic). Mandible with a very large dental plate on each side, meeting one, two, or three pairs of dental plates in the upper jaw. Gill clefts covered by a fold of skin, so that there is only one external opening. Vertebral axis not distinctly segmented, and the notochord surrounded by numerous partially calcified rings of cartilage. Paired fins with two or three short basal cartilages; pelvic fins of male with appended claspers.

The *Holocephali* occupy a unique position among the *Elasmobranchii*, on account of (1) the incompletely segmented character of the vertebral axis, in which the number of the cartilaginous rings considerably exceeds that of the arches and processes; and (2) the fusion of the upper jaw with the skull. Their trunk resembles that of the sharks, while the dentition is distinguished by the remarkably peculiar form and structure of the few very large dental plates. Of the four surviving genera: *Chimaera* lives off the European coasts, the various coasts of the Pacific, and the Cape of Good Hope; *Callorhynchus* in the seas of the southern hemisphere; *Harriotta* in the deep Atlantic off North America; and *Rhinochimaera* in deep water off Japan, and in the Indian Ocean. In all these genera the anterior dorsal fin is provided in front with a strong spine, which is supported by a broad plate of cartilage fixed to the vertebral column, and is united with this plate by a cartilage articulation. Besides the fin spine, the males of recent forms bear on the frontal region a spine which is rounded in front and covered with prickles, as well as smaller prickly spines in front of the pelvic fins. The long copulatory organs are also strengthened by thin calcified rods. The skin of the existing genera is naked, but in some extinct genera it is partly covered with shagreen granules and plates. A remarkable peculiarity of the Chimaeroids consists in the unusually conspicuous character of the mucus canals, which traverse the skin of the head and form the very prominent lateral line of the trunk. These are surrounded by numerous, closely arranged, calcified rings of cartilage.

FIG. 151.

Chimaera monstrosa Linn. Widely open mouth showing dentition of young fish, from the Mediterranean Sea. *md*, lower dental plates; *mx*, hinder upper dental plates; *n*, nasal cartilage; *pmx*, anterior upper dental plates. Nat. size.

The existing representatives of the *Holocephali* are only an insignificant remnant of a former much more extensively developed group of Elasmobranchs which appears first in the Lower Jurassic, and is perhaps genetically connected with the *Cochliodontidae*.

[1] *Dean, B.*, Chimaeroid Fishes. Carnegie Inst. Washington, Publ. no. 32, 1906.—*Garman, S.*, The Chimaeroids. Bull. Mus. Comp. Zool. Harvard, vol. xli., no. 2, 1904.—The Chismopnea (Chimaeroids). Mem. Mus. Comp. Zool. Harvard, vol. xl., no. 3, 1911.

Family 1. **Squaloraiidae.**[1]

Trunk depressed and elongated, and head produced into a long, slender snout. Lower dentition comprising one pair, upper dentition two pairs of thin corrugated dental plates without definite tritors. Males with a prehensile spine on the snout. Dorsal fin spine absent. Numerous conical or stellate dermal tubercles. Lower Jurassic.

Squaloraja Riley (*Spinacorhinus* Ag.). Tail tapering to a point. Rostral spine with expanded base, tapering to a point in front. Vertebral rings well calcified, consisting of several concentric lamellae. *S. polyspondyla* Ag. sp., known by nearly complete skeletons 45 cm. in length, from the Lower Lias of Lyme Regis, Dorset.

Family 2. **Myriacanthidae.**[2]

Trunk elongated. Two or three upper pairs and one lower pair of thin dental plates, also a stout, median, incisor-like tooth at the symphysis of the mandible. Head with a few dermal plates. Males with a prehensile spine on the snout. Anterior dorsal fin above the pectorals, with a long, straight, robust spine. Jurassic.

Myriacanthus Ag. (*Prognathodus* Egerton; *Metopacanthus* Zittel). Rostrum with a terminal cutaneous flap. Anterior upper dental plates smaller than the

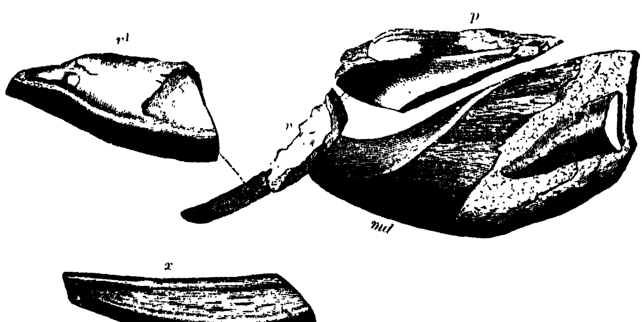


FIG. 152.

Chimaeropsis paradoxa Zitt. Upper Jurassic (Lithographic Stone); Eichstadt, Bavaria. 1/2 nat. size. *md*, mandibular dental plate; *p*, hinder upper dental plate; *r*, anterior upper dental plate in side view; *r*¹, same from lower side; *x*, slender premandibular (symphysial) tooth.

posterior plates. Dorsal fin spine long and slender, somewhat laterally compressed, with a large internal cavity; sides ornamented with small tubercles; a series of large, thorn-shaped tubercles arranged along each edge of the flattened posterior face, passing into a single median row distally, and a single series of similar denticles on the anterior border. Rostral spine elongated and pointed, with expanded base. Dermal plates tuberculated. *M. paradoxus* Ag., and *M. granulatus* Ag., from Lower Lias of Lyme Regis. A dorsal fin spine (*M. bollensis* E. Fraas) from Upper Lias, Holzmaden, Würtemberg. A dental plate from Inferior Oolite, Gloucestershire.

[1] *Reis, O. M.*, Geol. Mag. [4], vol. ii., p. 385, 1895.—*Woodward, A. S.*, Proc. Zool. Soc., 1886, p. 527; 1887, p. 481.

[2] *Woodward, A. S.*, Ann. Mag. Nat. Hist. [6], vol. iv., p. 275, 1889, and Quart. Journ. Geol. Soc., vol. lxii., p. 1, 1906.

Acanthorhina E. Fraas.[1] Rostrum hardened into a pointed spine. Rostral spine of male small, enamelled, curved, and pointed. Three pairs of upper dental plates. Dorsal fin spine slender, not tuberculated. *A. jaekeli* E. Fraas. Upper Lias; Holzmaden, Würtemberg.

Chimaeropsis Zittel[2] (Fig. 152). Mandibular dental plates (*md*), slightly arched, with a large tritoral area; the symphysial tooth (*x*) externally (inferiorly) convex, internally (superiorly) flat or concave. Anterior (*v*) and posterior (*p*) upper dental plates triangular, the former not smaller than the latter, and tapering in front, the latter tapering behind. Fin spine as in *Myriacanthus*. Body covered with small, conical, radiately grooved placoid scales. *C. paradoxa* Zittel, from Upper Jurassic (Lithographic Stone) of Bavaria.

Family 3. **Chimaeridae.** Chimaeras.[3]

Trunk elongated, shark-like. Teeth forming two pairs of robust dental plates in the upper jaw, the foremost the smaller, both pairs thickened and closely apposed in the longitudinal mesial line of the mouth; lower dentition comprising a single pair of beak-shaped plates meeting at the symphysis; the plates usually with several tritors. Pectoral fins very large, fan-like, with simple, horny rays; anterior dorsal fin above the pectorals, with a large spine articulated to a cartilaginous base; posterior dorsal fin low, much extended. Skin naked, or with shagreen granules. Jurassic to Recent.

Ischyodus Egerton[4] (*Leptacanthus* Ag.; *Auluxacanthus* Sauvage; *Chimaeracanthus* Quenstedt) (Fig. 153). Lower dental plates rhomboidal, with a narrow symphysial facet; upper part of outer face covered with a thick layer of dentine, and oral margin sharp; four rough punctate tritors present. Posterior upper dental plates triangular, tapering in front, with four tritors; anterior upper teeth square, antero-posteriorly compressed. Dorsal fin spine laterally compressed, smooth or longitudinally striated, with a double longitudinal series of denticles on the hinder face. Males with a short, arched head spine, bearing a cluster of denticles at the end. Nearly complete skeletons of *I. avitus* Meyer sp. (Fig. 153), and *I. quenstedti* Wagner, from the Lithographic Stone of Bavaria. Detached dental plates from the Bathonian (Stonesfield Slate) to the Upper Cretaceous of England, France, Germany, and Switzerland; from Portlandian, Moscow; also from Cretaceous of Amuri Bluff, New Zealand.

Ganodus Ag. Dentition as in *Ischyodus*, but posterior upper dental plate deeply excavated behind, with a double longitudinal series of numerous small tritors. Bathonian (Stonesfield Slate); England. *G. oweni* Ag., and other species.

Pachymylus A. S. Woodw.[5] Middle Jurassic (Oxford Clay); England.

Brachymylus A. S. Woodw.[5] (*Aletodus* Jaekel). Middle and Upper Jurassic (Oxford and Kimmeridge Clays); England. Lower Jurassic; Würtemberg.

[1] *Fraas, E.*, Jahresh. Vereins f. vaterl. Naturk. Württ., 1910, p. 55.

[2] *Riess, J.*, Palaeontographica, vol. xxxiv., p. 21, 1887.

[3] *Hussakof, L.*, Cretaceous Chimaeroids of North America. Bull. Amer. Mus. Nat. Hist., vol. xxxi., art. xix., 1912.—*Newton, E. T.*, Chimaeroid Fishes of British Cretaceous Rocks. Mem. Geol. Survey, mon. no. iv., 1878.

[4] *Ammon, L. von*, Ber. naturw. Vereins Regensburg, pt. v., p. 1, 1896.—Geogn. Jahresh., 1899, p. 1.—*Dean, B.*, Mem. Amer. Mus. Nat. Hist., vol. ix., pt. v., p. 259, 1909.—*Philippi, E.*, Palaeontographica, vol. xliv., p. 1, 1897.

[5] *Woodward, A. S.*, Ann. Mag. Nat. Hist. [6], vol x., p. 13, 1892.

Edaphodon Buckland (*Passalodon* Buckl.; *Eumylodus, Mylognathus* Leidy; *Dipristis* Marsh; *Bryactinus* Cope) (Fig. 154). Lower dental plates with a broad symphysial facet; posterior upper dental plates tapering in front, truncated behind, and with three tritors. Cretaceous and Eocene of Europe and North America. Also Oligocene and Miocene in Europe. *E. antwerpiensis* Leriche, Miocene, Belgium, is latest species.

Isotaenia, Leptomylus Cope. Cretaceous; New Jersey, U.S.A.

Elasmodectes Newton (*Elasmognathus* Newton *nec* Gill). Mandibular teeth laterally compressed and trenchant, with a series of small tritors along the oral border. *E. secans* A. S. Woodw., from Kimmeridge Clay, Weymouth. *E. willetti* Newton, from Lower Chalk, Kent.

Elasmodus Egerton. Upper Cretaceous of Belgium; Eocene of England and Prussia.

Amylodon Storms.[1] Upper Oligocene (Rupelian); Belgium. Perhaps identical with *Rhinochimaera* Garman, existing in sea off Japan.

Dental plates of the existing genus *Callorhynchus* Gronow have been identified from the Cretaceous of Amuri Bluff, New Zealand, and the Lower

FIG. 153.
Ischyodus avitus H. v. Meyer sp. Almost complete skeleton, 1/2 nat. size. Upper Jurassic (Lithographic Stone); Eichstädt (after H. v. Meyer).

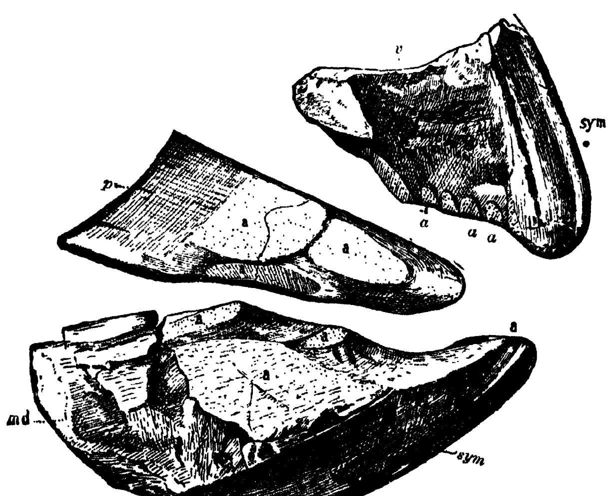


FIG. 154.
Edaphodon sedgwicki Ag. sp. Dental plates, 1/2 nat. size. Lower Chalk; Lewes. *md*, left mandibular dental plate, inner aspect; *p*, left hinder upper dental plate, oral aspect; *v*, left anterior upper dental plate, inner aspect; *a*, tritors; *sym*, symphysial border (after E. T. Newton).

Tertiary (Patagonian Formation) of Santa Cruz, Argentina; of the existing

[1] *Storms, R.*, Bull. Soc. Belge Géol., etc, vol. viii., p. 71, 1895.

genus *Chimaera* Linn., from the Eocene of England, the Oligocene of Belgium (*C. gosseleti* Winkler sp.), and the Upper Tertiary of Europe, Australia, New Zealand, and Java.[1]

Fossil eggs of Chimaeroids have been described from the Lower Jurassic of Würtemberg,[2] the Upper Jurassic of Verdun (Meuse),[3] and the Upper Cretaceous of Wyoming, U.S.A.[4]

Ichthyodorulites.

Fossil fin spines consisting of vasodentine, and thus presumably referable to the *Elasmobranchii*, are frequently found isolated especially in the Palaeozoic formations, and can only be in part assigned to definite genera. These are therefore described under provisional generic names. Most of them are bilaterally symmetrical, and may be regarded as median dorsal spines; but several are distinctly rights and lefts, and belong either to the paired fins, as in *Acanthodidae*, or to the side of the head, as in *Menaspis* among *Cochliodontidae*. In the unsymmetrical spines the base is, as a rule, abruptly truncated; in the bilaterally-symmetrical dorsal spines it is usually elongated and tapers to the proximal end.

FIG. 155.
Onchus tenuistriatus Ag. Fin spine, nat. size. Upper Silurian; Ludlow, England.

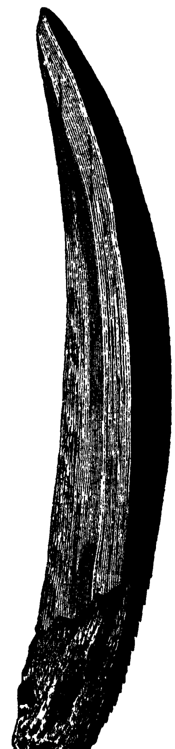


FIG. 156.
Machaeracanthus major Newberry. Middle Devonian; Sandusky, Ohio. 1/2 nat. size (after Newberry).

Among the Ichthyodorulites not yet referable with certainty to definite genera or families, the following may be enumerated:

(*a*) Slender, bilaterally-symmetrical spines, with a smooth base sharply separated from the exserted portion; internal cavity open posteriorly towards the base. *Onchus* Ag.[5] (Fig. 155); Upper Silurian and Devonian, Europe and eastern North America. *Homacanthus* Ag.; Devonian and Lower Carboniferous. *Striacanthus* Hills; Upper Devonian, Victoria, Australia. *Acondylacanthus* St. J. and Worth.; *Asteroptychius* M'Coy; *Lispacanthus* Davis; *Geisacanthus* St. J. and Worth.; Lower Carboniferous. *Lepracanthus* Owen; British Coal Measures.

(*b*) Slender, bilaterally symmetrical spines, with little or no smooth inserted portion, and internal cavity only open at the proximal end. *Gnathacanthus* Davis. Lower Carboniferous; Armagh, Ireland. *Pristacanthus* Ag. Bathonian; Oxfordshire and Normandy.

1 *Woodward, A. S.*, and *White, E. I.*, Ann. Mag. Nat. Hist. [10], vol. vi., p. 577, 1930.
2 *Jaekel, O.*, Neues Jahrb. f. Min., Beil.-Bd. xiv., p. 540, 1901.
3 *Leriche, M.*, Ann. Soc. Roy. Zool. Malacol. Belg., vol. xlviii., p. 145, 1914.
4 *Dean, B.*, Mem. Amer. Mus. Nat. Hist., vol. ix., pt. v., p. 265, 1909.
5 For microscopic structure, see *Rohon, J. V.*, Mém. Acad. Imp. Sci. St.-Pétersb., ser. 7, vol. xli., no. 5, p. 38, 1893.

(c) Right and left paired spines, most probably connected with fins. *Machaeracanthus* Newb. (Fig. 156); *Heteracanthus* Newb. (*Gampsacanthus* S. A. Miller); *Haplacanthus* Ag. Devonian; Europe and North America.

(d) Paired spines, usually with a broad, truncated base, a large internal cavity, and the outer face tuberculated. Probably lateral head spines, as in *Menaspis* among *Cochliodontidae*. *Oracanthus* Ag. (*Platyacanthus* M'Coy; *Pnigeacanthus* St. J. and Worth.; *Phoderacanthus* Davis). Carboniferous of Europe and North America (spines already observed on either side of head in one example of *Deltoptychius*, see p. 88). *Physonemus* M'Coy; *Xystracanthus* Leidy (perhaps Edestid, see p. 65); *Drepanacanthus* Newb.; *Erismacanthus* M'Coy; *Gampsacanthus* St. J. and Worth (Fig. 157); *Lecracanthus* St. J. and Worth.; *Dipriacanthus* M'Coy; *Stichacanthus* Koninck, etc. Lower Carboniferous.

(e) Spines of entirely doubtful position. *Cynopodius* Traquair. Lower Carboniferous; Scotland. *Eunctenius* Traquair. Coal Measures; Scotland, England, and Ohio, U.S.A. *Listracanthus* Newb. and Worth. (found associated with dermal tubercles named *Petrodus* M'Coy or *Ostinaspis* Trautschold).[1] Coal Measures; Illinois, Indiana, and Ohio, U.S.A., also Lancashire and Staffordshire, England. Lower Carboniferous; Belgium, Germany, and Scotland. *Stethacanthus* Newb. Upper Devonian and Lower Carboniferous; Ohio, Illinois, and Iowa.

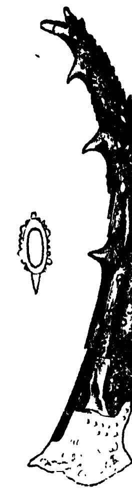


FIG. 157.
Gampsacanthus typus St. John and Worthen. Carboniferous Limestone; St. Louis, Missouri (after St. John and Worthen).

Sub-Class 5. DIPNOI.[2] Lung-fishes.

Skeleton partially ossified, with numerous well-developed membrane bones. A parasphenoid bone. Pterygoquadrate arcade completely and immovably fused with the cranium (autostylic); gill clefts feebly separated, opening into a cavity covered with a bony operculum. Dentition powerful for crushing. Paired fins paddle-like, with a long, segmented cartilaginous axis (archipterygium of Gegenbaur); tail diphycercal, heterocercal, or gephyrocercal, but fin usually with an upper lobe. In the living forms—optic nerves not decussating but forming a chiasma, bulbus arteriosus of the heart with numerous valves, intestine with a spiral valve, and air bladder lung-like.

The internal skeleton of the *Dipnoi* is chiefly cartilaginous, but the upper and lower vertebral arches, the ribs and fin supports, all exhibit some superficial ossification.

[1] *Woodward, A. S.*, Geol. Mag. [4], vol. x., p. 486, 1903.

[2] *Bridge, T. W.*, Morphology of the Skull in the Paraguayan *Lepidosiren* and in other Dipnoids. Trans. Zool. Soc., vol. xiv., p. 325, 1898.—*Dollo, L.*, Sur la phylogénie des Dipneustes. Bull. Soc. Belge Géol., etc., vol. ix., Mém., p. 79, 1895.—Sur un Dipneuste nouveau . . . dans le Dévonien supérieur de la Belgique. Bull. Acad. Roy. Belg., Classe Sci., 1913, p. 15.—*Goodrich, E. S.*, On the Cranial roofing-bones in the Dipnoi. Journ. Linn. Soc.—Zool., vol. xxxvi., p. 79, 1925.—*Günther, A.*, Description of *Ceratodus*. Phil. Trans. Roy. Soc., vol. clxi., p. 511, 1871.—*Huxley, T. H.*, On *Ceratodus*. Proc. Zool. Soc., 1876, p. 24.—*Miall, L. C.*, Monograph of the Sirenoid and Crossopterygian Ganoids. Palaeont. Soc., 1878.—*Pander, C. H.*, Über die Ctenodipterinen, etc., des devonischen Systems. St. Petersburg, 1858.—*Traquair, R. H.*, On the genera *Dipterus*, *Palaedaphus*, *Holodus*, and *Cheirodus*. Ann. Mag. Nat. Hist. [5], vol. ii., p. 1, 1878.—*Watson, D. M. S.*, and *Day, H.*, Notes on some Palaeozoic Fishes. Mem. Manchester Lit. and Phil. Soc., vol. lx., no. 2, 1916.—*Watson, D. M. S.*, and *Gill, E. L.*, The Structure of certain Palaeozoic Dipnoi. Journ. Linn. Soc.—Zool., vol. xxxv., p. 163, 1923.

The *Dipnoi* differ from all other existing fishes, in the modification of the air bladder into a single or double elongated sac with numerous cellular spaces, which serves as a lung and is connected by a short tube with the anterior wall of the gullet; moreover, in the peculiar characters in the structure of the heart, in the presence of internal narial openings, and in the possession of the faculty of existing for a considerable period out of water. They were therefore at first regarded as fish-like Amphibians or scaly Sirens. The discovery of the "Barramunda" (*Ceratodus forsteri*) in the rivers of Queensland confirmed the idea of their relationship to the Palaeozoic Crossopterygians previously suggested by Huxley. Nevertheless, they are distinguished from these and from all other Ganoids and Teleosteans by the autostylic arrangement of the jaws and the peculiar dentition.

Family 1. **Dipteridae.**

Cranial roof bones small and numerous, covered with cosmine. A pair of dental plates on the pterygopalatine bones, and an opposing pair on the splenials; these plates usually retaining traces of their component denticles. Jugular plates present, including a median plate. Tail heterocercal: dorsal and anal fins separate. Scales cycloidal, deeply overlapping, and their exposed portion covered with cosmine. Devonian.

Dipterus Sedgw. and Murch. (*Catopterus*, *Polyphractus* Ag.; *Pentlandia* Watson and Day; *Paradipterus* Jaekel) (Figs. 158, 159). Base of cranium

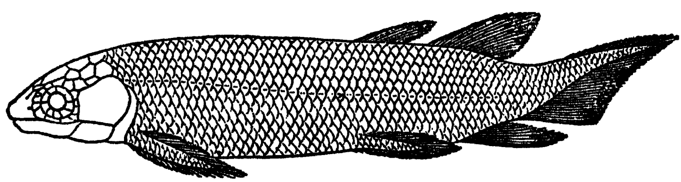


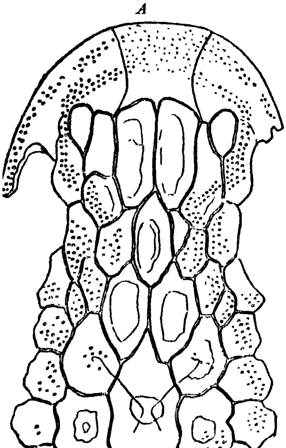
Fig. 158.
Dipterus valenciennesi Sedgw. and Murch. Restoration by Traquair, about 1/4 nat. size. Middle Old Red Sandstone; Scotland.

covered with a toothless, broad, rhombic parasphenoid (*PSph*), which is flanked on either side by a pterygopalatine (*P*) extending forwards, meeting in the middle in a straight line and forming a triangular pointed plate, which serves as base for a large triangular dental plate (*d*) bearing tuberculated radiating ridges. The mandible is well ossified, with a single, large dental plate on the splenial of each side, and its tuberculated ridges radiating fan-like from within outwards. Two pairs of large jugular plates. Paired fins acutely lobate, the pelvic pair remote and opposed to the anterior of the two dorsal fins; anal fin opposite the posterior dorsal. Scales nearly rhombic in their exposed portion. Complete, but mostly flattened and distorted examples of *Dipterus valenciennesi* Sedgw. and Murch., sometimes nearly half a metre long, are not uncommon in the Middle Old Red Sandstone of northern Scotland. Dental plates very abundant in Middle and Upper Devonian of central and eastern United States; also found in the Devonian of Belgium, North Russia, and Novaia Zemlya.

Palaedaphus van Beneden (*Heliodus* Newb.) (Fig. 160). Only known by mandible and detached dental plates. In *P. insignis* van Ben. and de Koninck,

each lower dental plate, measuring 17 cm. in length, bears four smooth, obtuse radiating ridges. Upper Devonian; Belgium, N. France, and Pennsylvania (*P. lesleyi* Newb. sp.).

Ganorhynchus Traquair (*Dipnorhynchus* Jaekel). Bones of end of snout fused together; a row of



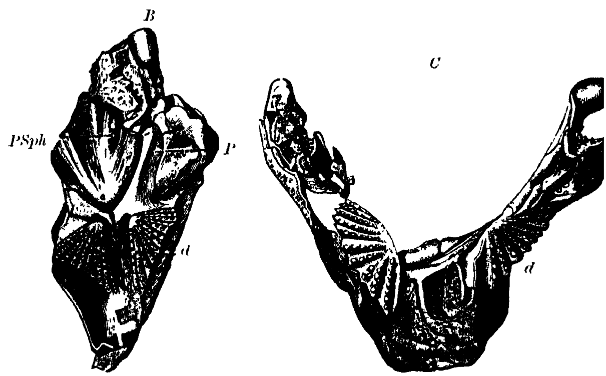


FIG. 159.

Dipterus valenciennesi Sedgw. and M. Middle Old Red Sandstone; Banniskirk. *A*, Roof of skull. *B*, Imperfect palate (*PSph*, parasphenoid; *P*, pterygopalatine, accidentally divided into two pieces behind by a broken line; *d*, palatine dental plate). *C*, Imperfect mandible with dental plate (*d*) (after Pander).

tubercles sometimes present on the edge between the inferior notches for the narial openings. *G. woodwardi* Traq., history unknown. *G. rigauxi* Dutertre, from Upper Devonian, N. France. *G. beecheri* Newberry, from Upper Devonian (Chemung), Pennsylvania, U.S.A. *G.* (*Dipnorhynchus*) *sussmilchi* Etheridge, a skull from Devonian, Murrumbidgee River, New South Wales.[1]

Eoctenodus Hills.[2] Perhaps identical with *Dipterus*. Upper Devonian; N. W. Gippsland, Victoria, Australia.

Conchodus M'Coy. Dental plates thin, almost smooth, with a few short radiating ridges at the outer border. *C. ostreaeformis* M'Coy, from Upper Old Red Sandstone, Elgin. Other plates from Devonian, N. Russia and Latvia.

Synthetodus Eastman. Upper Devonian; Iowa, U.S.A.

Holodus Pander. Devonian; Orel, Russia.

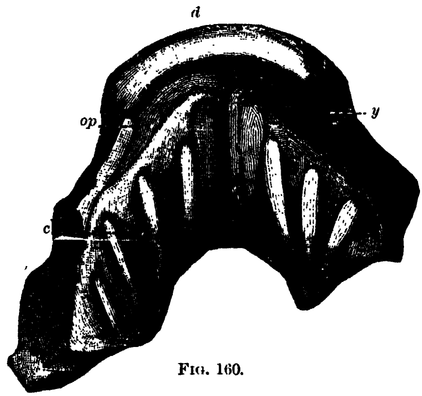


FIG. 160.

Palaedaphus insignis van Beneden and de Koninck. Imperfect mandible, 1/4 nat. size. Devonian; Liège. *c*, dental plate; *d*, dentary; *op*, splenial; *y*, lateral fossa (after Traquair).

Family 2. Uronemidae.[3]

Upper dentition consisting of small, blunt, conical denticles on the pterygopalatine bones; lower dentition of similar denticles on the splenial. Median fins

[1] *Etheridge, R.*, Rec. Australian Mus., vol. vi., p. 129, 1906.

[2] *Hills, E. S.*, Proc. Roy. Soc. Victoria, vol. xli., p. 193, 1929; also Geol. Mag., 1931, p. 222.

[3] *Weitzel, K.*, *Conchopoma gadiforme* Kner, ein Lungenfisch aus dem Rothliegenden. Abhandl. Senckenberg. Naturf. Ges., vol. xl., p. 159, 1926.

continuous and tail diphycercal or gephyrocercal. Lower Carboniferous to Lower Permian (? Lower Trias).

Uronemus Ag. (*Ganopristodus* Traq.). Body laterally compressed, with small and very thin scales, which are faintly striated. Paired fins acutely lobate. Dorsal fin arising shortly behind the head. Parasphenoid toothless; a row of laterally compressed conical teeth, larger than the tubercular teeth, along the edge of the pterygopalatine and splenial bones. *U. lobatus* Traq. and *U. splendens* Traq. from Lower Carboniferous, near Edinburgh.

Conchopoma Kner. Parasphenoid with tubercular teeth. Lower Permian; Rhenish Prussia. *Peplorhina* Cope. Coal Measures; Linton, Ohio.

? *Gosfordia* A. S. Woodw. Head very small. Body laterally compressed, with small and very thin scales, which are striated. *G. truncata* A. S. W., from Hawkesbury Beds (Lower Triassic), New South Wales, Australia.

Family 3. Phaneropleuridae.[1]

Cranial roof bones small and numerous, not enamelled. A row of teeth on premaxilla and maxilla; dental plates as in Dipteridae. *A single pair of jugular plates. Tail diphycercal, gephyrocercal or heterocercal, and dorsal fins almost or completely continuous with it. Scales thin and cycloid, deeply overlapping, the outer layer of the exposed portion reduced to spinelets.* Upper Devonian.

Phaneropleuron Huxley. Upper dental plates triangular, with straight and crenulated radiating ridges. Long dorsal fin continuous with the caudal,

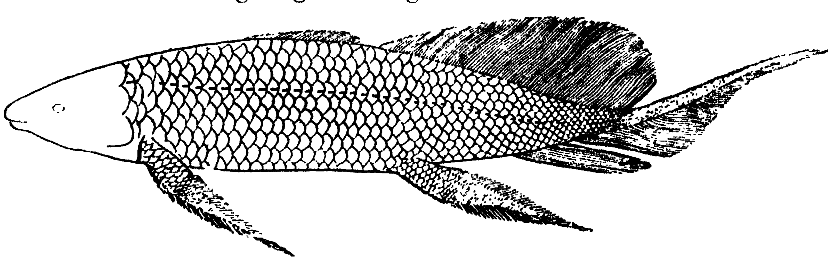


FIG. 161.
Scaumenacia curta Whiteaves sp. Restoration by Hussakof, $^2/_3$ nat. size. Upper Devonian; Scaumenac Bay, Quebec.

but small anal fin separate. Scales marked with delicate radiating striae. *P. andersoni* Huxl., known by well-preserved specimens 30 cm. long from Upper Old Red Sandstone, Fifeshire.

Scaumenacia Traquair (*Canadipterus* Jaekel) (Fig. 161). Two extended dorsal fins, as well as the anal fin, separate. *S. curta* Whiteaves sp., from Upper Devonian, Scaumenac Bay, Quebec, Canada.

Family 4. Ctenodontidae.

Cranial roof bones numerous, not enamelled. No marginal teeth; dental plates as in Dipteridae. *Jugular plates reduced or absent. Tail diphycercal or gephyrocercal, and dorsal fins continuous with it. Scales large, thin and cycloid, deeply overlapping, the exposed portion marked with a coarse reticulation.* Carboniferous and Permian (? Lower Trias).

[1] *Hussakof, L.*, Devonic Fishes from Scaumenac Bay, Quebec. New York State Mus. Bull. 158, p. 127, 1912.

Ctenodus Ag. (Fig. 162). Hinder border of cranial roof with one median occipital plate, with a pair of plates immediately adjoining in front. Dental plates with numerous tuberculated or crenulated radiating ridges. Dorsal and anal fins continuous with the caudal; scales almost quadrate in shape, but with rounded angles. *C. cristatus* Ag. Dental plates common in the Carboniferous of Europe and North America; fine portions of skeleton in the English Coal Measures. *C. breviceps* A. S. Woodw., skull from Carboniferous of Victoria, Australia.

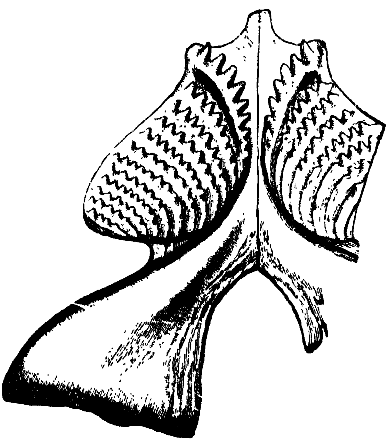


FIG. 162.

Ctenodus cristatus Ag. Pterygopalatine with dental plates, 1/3 nat. size. Coal Measures; Newsham, Northumberland (after Hancock and Atthey). Oral surface of dental plates really concave.

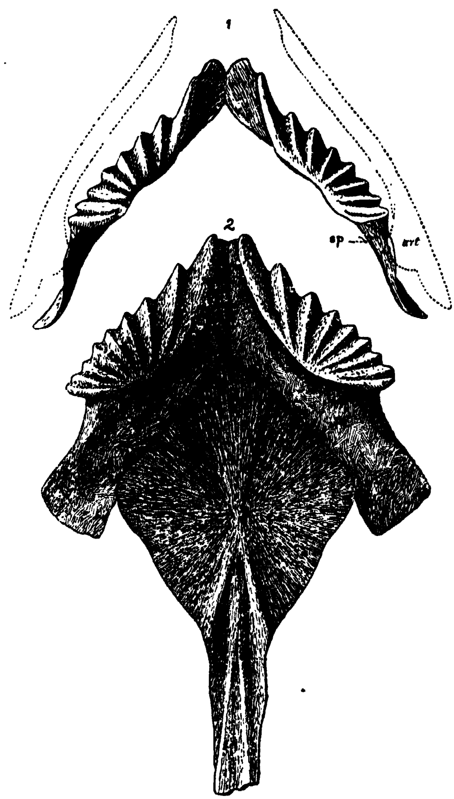


FIG. 163.

Sagenodus copeanus Williston. Lower (1) and upper (2) jaws with dental plates. Coal Measures; Kansas. *art*, articular; *ps*, parasphenoid; *pt*, pterygopalatine; *sp*, splenial. After Williston.

Sagenodus Owen [1] (*Megapleuron* Gaudry; *Ptyonodus* Cope) (Fig. 163). As *Ctenodus*, but dental plates with fewer ridges, and median occipital plate with another unpaired plate immediately in front of it. *S. inaequalis* Owen. Scales and dental plates common in the Carboniferous and Lower Permian of Europe and North America; fine skeletons in the Lower Permian of Bohemia and France. *S. laticeps* A. S. Woodw. (? *Ceratodus*); portions of fish from Triassic, New South Wales.

Gnathorhiza Cope. Comparatively small dental plates, with very sharp, compressed, radiating ridges, three in the lower, four in the upper plate. *G. pusilla* Cope sp. Permian; Illinois, Texas, and Oklahoma. Upper Permian or Lower Triassic; Vologda, Russia.

[1] *Williston, S. W.*, Kansas Univ. Quart., vol. viii., p. 175, 1899.

Family 5. Ceratodontidae.

Cranial roof bones few, thin and not enamelled. No marginal teeth. A pair of dental plates on the pterygopalatine bones, and an opposing pair on the splenials; also a pair of small cutting teeth on the vomer. Jugular plates absent. Paired fins acutely lobate and scaly. Median fin continuous, and tail diphycercal or gephyrocercal. Body covered with large, thin, elastic, cycloid scales without a bony basis. Triassic to Recent.

Ceratodus Ag. (*Hemictenodus* Jaekel; *Metaceratodus* Chapman) (Figs. 164, 165).[1] The pectoral and pelvic fins are fringed with membrane stiffened by fine rays. The upper vertebral arches, spinous processes, ribs, and fin supports are superficially ossified. The flattened roof of the skull consists of two

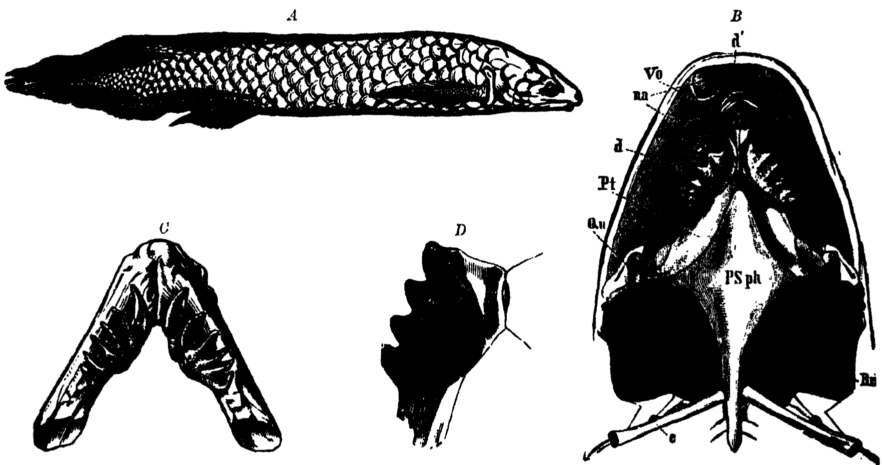


FIG. 164.

Ceratodus forsteri Krefft. Lateral aspect of fish (*A*), base of skull (*B*), and mandible (*C*), reduced. Recent; Queensland. *Br*, branchial cavity; *c*, foremost rib; *d*, dental plates; *na*, nasal openings; *PSph*, parasphenoid; *Pt*, pterygopalatine; *Qu*, quadrate; *Vo*, vomer (after Günther); *D*, *Ceratodus kaupi* Ag. Mandibular dental plate on bony base, 1/3 nat. size. Lettenkohle; Hoheneck, near Ludwigsburg.

large median plates, one behind the other, and two pairs of lateral plates. On the lower side of the chondrocranium there occurs the long parasphenoid (*PSph*), with its rhombic anterior expansion flanked on either side by the pterygopalatines (*Pt*). The latter bones meet in a median suture in front, and each bears a large triangular dental plate (*d*), with radiating ridges. The vomerine cartilage (*Vo*) bears a pair of sharp, chisel-shaped teeth (*d'*) (not yet seen in fossils). On the splenial of each ramus of the mandible there is also a dental plate with deep, radiating ridges. The opercula, sub-opercula, hyoid bones, and branchial arches are ossified; the quadrate (*Qu*) remains cartilaginous.

[1] *Chapman, F.*, New Species of *Ceratodus* from the Cretaceous of New South Wales. Proc. Roy. Soc. Victoria, n.s., vol. xxvii., pt. i., 1914.—*Longman, H. A.*, Notes on *Epiceratodus*. Mem. Queensland Mus., vol. ix., p. 160, 1928.—*Stromer, E. von*, and *Peyer, B.*, Über rezente und triassische Gebisse von Ceratodontidae. Zeitschr. Deutsch. Geol. Ges., vol. lxix., p. 1, 1917.—*Teller, F.*, Über *Ceratodus sturi*. Abh. k. k. geol. Reichsanst. Wien, vol. xv., 1891.—*White, E. I.*, Fossil *Epiceratodus* from West Australia. Ann. Mag. Nat. Hist. [9], vol. xvi., p. 139, 1925; New South Wales, *loc. cit.*, vol. xvii., p. 677, 1926.—*Zittel, K. A. von*, Über *Ceratodus*. Sitzb. k. Bay. Akad. Wiss., math.-phys. Cl., 1886.

In the living *Ceratodus* (*Neoceratodus* Castelnau; *Epiceratodus* Teller) the upper and lower dental plates bear six ridges radiating outwards. The corresponding plates occurring in the Trias, namely, in the bone-beds of the Muschelkalk, Lettenkohle, and Rhaetic, are distinguished by their larger size and a different number of ridges. As a rule, the upper dental plates exhibit five, the lower only four radiating ridges. The oldest known species (*C. arenaceus* Quenst., *C. priscus* E. Fraas) are from the Bunter Sandstone of Germany. The largest teeth occur in the Keuper (*C. runcinatus* Plien.) (Fig. 165) and Rhaetic (*C. latissimus* Ag.) of Europe. A well-preserved skull (*C. sturi* Teller) from the Upper Keuper of Polzberg, near Lunz, Lower Austria, is more ossified than the skull of the existing *Ceratodus*. Of the same age are teeth found in Spitzbergen, Arizona, New Mexico, and Texas (U.S.A.), in the Kota-Maleri beds of India (*C. hislopianus* Oldham) and the Karroo Formation of South Africa (*C. capensis* A. S. Woodw., *C. ornatus* Broom, *C. kannemeyeri* Seeley). Small teeth occur in the Bathonian of England (*C. phillipsii* Ag.), the Jurassic of Madagascar (*C. madagascariensis* and *C. acutus* Priem), the Lower Jurassic of Victoria, Australia (*C. avus* A. S. Woodw.), and the Jurassic of Colorado and Wyoming, U.S.A. (*C. guentheri* Marsh, *C. americanus* Knight); others in the Cretaceous of Egypt (*C. humei* Priem), Central Africa (*C. africanus* Haug), Patagonia (*C. iheringi* Ameghino), and New South Wales (*C. wollastoni* Chapman). Extinct species in the Pleistocene of Australia.

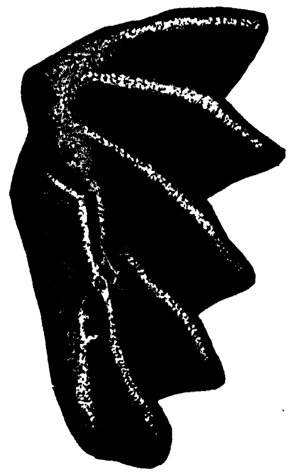


FIG. 165.
Ceratodus runcinatus Plieninger. Upper dental plate, nat. size. Lettenkohle; Hoheneck.

Family 6. **Lepidosirenidae.**[1]

Cranial roof bones much reduced, thin and not enamelled. Dental plates with well-separated ridges. Body much elongated, median fin continuous, and tail diphycercal or gephyrocercal. Paired fins reduced to rod-shape. Scales small. Tertiary and Recent.

Lepidosiren Natterer. Living in fresh-waters of South America.

Protopterus Owen. Living in fresh-waters of tropical Africa. Dental plates from Oligocene of the Fayum, Egypt (*P. libycus* Stromer), and Lower Miocene of British East Africa.

Sub-Class 6. GANOIDEI.[2] Enamel-scaled Fishes.

Trunk and tail usually covered with ganoid scales, rarely naked or with bony plates. Skull covered with dermal bones, or completely ossified; a parasphenoid bone;

[1] *Stromer, E.*, Gebiss der Lepidosirenidae. Festschr. f. R. Hertwig, vol. ii., 1910. Also Zeitschr. Deutsch. Geol. Ges., vol. 66, Monatsb., p. 420, 1914.

[2] *Cope, E. D.*, Trans. Amer. Phil. Soc., vol. xiv., p. 445, 1871; and Amer. Nat., vols. xix., xx., xxi., xxiii., 1885-89.—*Kner, R.*, Betrachtungen über die Ganoiden als natürliche Ordnung. Sitzungsb. k. Akad. Wiss. Wien, math.-naturw. Cl., vol. liv., 1866.—*Lütken, Chr.*, Über die

pterygoquadrate arcade movably articulated with the cranium (hyostylic); mandible more or less complex; gill clefts feebly separated, opening into a cavity covered with a bony operculum. Vertebral column cartilaginous, or with various degrees of ossification. Fin rays articulated, and fulcra usually present. Paired fins well developed; tail diphycercal, gephyrocercal, heterocercal, or hemi-heterocercal. In the living forms—optic nerves not completely decussating but forming a chiasma, bulbus arteriosus of the heart with numerous valves, intestine with a spiral valve, and air bladder connected by a tube with the gullet.

When founding the "Order" of Ganoids, Agassiz paid attention exclusively to the dermal skeleton, and included under this denomination all fishes with scales which consisted of a bony lower layer and a superficial covering of enamel or ganoine.

Johannes Müller first attempted to define the Ganoids from anatomical characters. After the removal of the *Plectognathi*, *Lophobranchii*, and *Siluroidei*, recognised as true bony fishes, and after the assignment of *Lepidosiren* to the *Dipnoi*, there still remained as true Ganoids a large number of recent and fossil fishes, which, according to Johannes Müller, formed a distinct Sub-Class between the *Elasmobranchii* and the bony fishes. While the condition of the muscular bulbus arteriosus, the incomplete decussation of the optic nerves, and the spiral valve in the intestine, agree with the former, the arrangement of the head bones, the structure of the fins, and usually also the ossification of the skeleton, are suggestive of the bony fishes. After C. Vogt had recognised in the anatomical structure of *Amia* a true Ganoid, with thin elastic cycloid scales and a completely ossified skeleton, the line of demarcation between the *Ganoidei* and *Teleostei* seemed to have been absolutely destroyed. Kner, Thiollière, Owen, and more recently Cope and A. S. Woodward, have ventured still further, suppressing the *Ganoidei* as a separate group, and uniting its members with the *Teleostei* under the general denomination of *Teleostomi*.

The most conspicuous, even if not the distinctive, feature of the Ganoids consists in their dermal covering. Except some of the early *Dipnoi*, no other fishes possess scales which consist of a thick bony inner layer and an outer enamel layer. In no other group is there a union of scales by peg-and-socket articulations, such as is characteristic of the rhombic-scaled Ganoids. There are, however, ganoid scales of rounded form, which overlap each other exactly like cycloid and ctenoid scales, and which are sometimes not perceptibly thicker than the latter; but these rounded scales (*Caturus*, *Megalurus*, *Oligopleurus*, *Amia*) exhibit beneath the enamel covering an inner layer with bone cells, though sometimes its thickness is excessively reduced. The Spatularias are characterised by the complete absence of scales, except on the upper lobe of the tail; in the Sturgeons the body is partly covered with large bony plates.

The structure of the internal skeleton of the Ganoids is of special interest, notably that of the vertebral column. In some *Chondrostei* (*Acipenser*) the vertebral axis, with its arches and spines, remains completely cartilaginous; but

Begrenzung und Eintheilung der Ganoiden. Palaeontogr., vol. xxii., 1868.—*Müller, Joh.*, Über den Bau und die Grenzen der Ganoiden. Abhandl. k. Akad. Wiss., Berlin, 1834, 1836.—*Stromer, E.*, Der Rückgang der Ganoidfisch von der Kreidezeit an. Zeitschr. Deutsch. Geol. Ges., vol. lxxvii., Abh. p. 348, 1925.—*Vogt, C.*, Quelques observations qui servent à la classification des Ganoides. Ann. Sci. Nat., Zool., ser. 3, vol. iv., 1845.—*Woodward, A. S.*, Fossil Fishes of Upper Lias of Whitby. Proc. Yorks. Geol. Polyt. Soc., vol. xiii., 1895-98.

in *Spatularia*, the older *Crossopterygii*, almost all *Palaeoniscidae* and *Platysomidae*, and part of the *Protospondyli*, there is a partial or complete ossification of the arches, spinous processes, and supports of the median fins, this beginning at the surface and extending inwards, so that a cartilaginous core is usually surrounded by a hollow bony cylinder. Rarely, when there are no ossified vertebrae, the arches expand proximally to surround the notochord (Fig. 166). More usually (Fig. 167) there develops below the notochord a horseshoe-shaped bony plate (*hypocentrum*, *intercentrum*), to which the haemal arch in the caudal region is fixed; the upwardly directed side-pieces of these hypocentra are

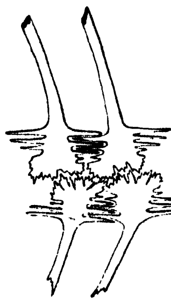


Fig. 166.

Two caudal vertebrae of *Pycnodus platessus* Ag. (after Heckel).

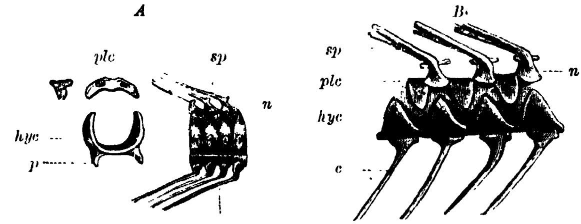


Fig. 167.

Vertebrae of *Euthynotus* (*A*), and *Caturus furcatus* Ag. (*B*). *c*, rib or haemal arch; *hyc*, hypocentrum; *n*, neural arch; *p*, parapophysis; *plc*, pleurocentrum; *sp*, cleft neural spine.

mostly attenuated and pointed. The vertebral centrum proper is represented by a pair of lateral bony plates (*pleurocentra*), which are usually pointed below and frequently fused together dorsally, thus forming a second horseshoe-shaped half ring. According to their size the hypocentra and

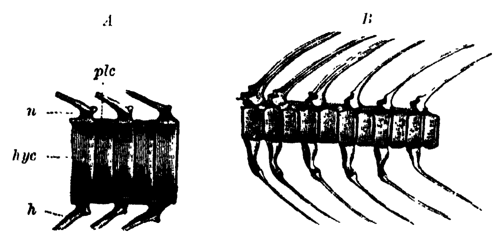


Fig. 168.

A, Caudal vertebrae of *Eurycormus speciosus* Wagn. *B*, vertebrae of *Amia calva* Linn., from anterior part of caudal region. *h*, haemal arch; *hyc*, hypocentrum; *n*, neural arch; *plc*, pleurocentrum.

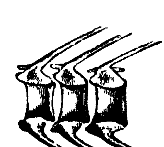


Fig. 169.

Aspidorhynchus sp. Caudal vertebrae, each bearing a neural and haemal arch.

pleurocentra more or less completely surround the soft, unsegmented notochord. Sometimes when the upper and lower lateral pieces do not taper but continue of uniform width, and meet together dorsally and ventrally, they form two narrow rings, which completely enclose the notochord (Fig. 168). In some genera (*Eurycormus*) the anterior abdominal region consists of half vertebrae, while the caudal region consists of ring vertebrae, which are composed of two halves (Fig. 168). By the complete fusion of the two half rings there arise simple, sheath-like ring vertebrae (Fig. 169). In the *Amiidae* the vertebral centra of the abdominal region are completely ossified and biconcave (*amphicoelous*), while some of those of the caudal region are still

divided into two halves, which correspond with the hypo- and pleuro-centra (Fig. 168, *B*).

The complete ossification of the vertebral column, as in the bony fishes, is observed only among the latest representatives of the Ganoids, namely, the *Polypteridae* and the *Lepidosteidae*. Among the latter, moreover, the vertebral centra are only concave behind, convex in front (*opisthocoelous*).

The hinder end of the vertebral column is always produced into the caudal fin. The true *diphycercal* condition (see p. 12) constantly persists in some Crossopterygians (*Coelacanthidae*) and Chondrosteans (*Belonorhynchidae*). In most Crossopterygians the caudal fin is *hetero-diphycercal*, that is, the vertebral column extends straight, but the rays of the upper lobe of the fin are more delicate and shorter than those of the lower lobe. True *heterocercy* and *hemi-heterocercy* (internal heterocercy, external homocercy, see p. 12) are very common.

In many Ganoids the unpaired fins, and sometimes also the paired fins, are fringed on the anterior border with the so-called *fulcra*—scale-like spines or plates covered with enamel, which are serially arranged and partly overlap one another. All the fin rays consist of two (right and left) halves, and are transversely jointed, usually also branched distally.

Like the vertebral column, the skull also exhibits very variable degrees of ossification. In the cartilaginous Ganoids this is almost exclusively confined to a number of investing plates on the cranial roof and the basicranial axis. The pterygoid and palatine bones are still fused together; the mandible and parts of the hyoid apparatus are ossified; the opercular apparatus is feebly developed. In the *Crossopterygii*, Palaeozoic *Chondrostei*, and *Protospondyli*, the ossification closely resembles that of the *Teleostei*, while the number and arrangement of the several bones agree essentially with the corresponding features in some of the least specialised members of the latter Sub-Class.

In the structure of the pectoral arch, and especially of the anterior limbs, the various Orders of Ganoids exhibit considerable differences, and represent intermediate links between the *Dipnoi*, *Elasmobranchii*, and *Teleostei*. In the *Crossopterygii* and *Chondrostei* the clavicular arch on each side consists of three membrane bones, usually separate; while in the *Protospondyli* and *Halecostomi* the lower segment (*clavicle*) disappears.[1] The small structures behind and within the middle and largest segment (*cleithrum*) corresponding with *scapula*, *coracoid*, and *precoracoid* or *mesocoracoid*, remain cartilaginous in the *Chondrostei*, probably also in the fossil *Crossopterygii*; in the rest of the Ganoids, on the other hand, they are ossified exactly as in the *Teleostei*. Moreover, in the position and number of the basal supports in the pectoral fins, most Ganoids agree with the bony fishes; the earlier *Crossopterygii* alone possessed a segmented cartilaginous axis, with biserial radialia, as in the *Dipnoi*.

Besides the anatomical characters in the dermal covering and the internal skeleton there are still others indicating that the Ganoids are a natural group of fishes. For example, the somewhat elongated muscular base of the principal artery (*bulbus arteriosus*) is provided internally, as in the *Elasmobranchii*, with several rows of valves, which prevent the return of the blood from the artery to the ventricle of the heart. The gills, on the other hand, as in the *Teleostei*, always lie free under an operculum, which usually consists of several bony plates. Again, by the possession of a spiral valve in the intestine, as well

[1] Zittel agreed with his contemporaries in naming the lower segment *infraclavicle*, the large upper segment *clavicle*.

as in the structure of the urinogenital system, the Ganoids approach the *Elasmobranchii* more closely than the *Teleostei*; on the other hand, they all possess an air bladder opening into the gullet, and also produce numerous small eggs. By the complete decussation of their optic nerves, the *Teleostei* are distinguished from the *Ganoidei*, in which the branching optic nerves form a so-called chiasma.

The Ganoids exhibit their greatest development in Palaeozoic, Triassic, and Jurassic formations; and from the base of the Cretaceous system upwards they become more and more replaced by the bony fishes. The few still existing Ganoids live either exclusively, or at least partly, in fresh water, while the large majority of the fossil forms occur in purely marine deposits. As a rule, only the Devonian and Tertiary Ganoids occur in fresh-water formations.

The *Ganoidei* may be divided into four Orders: (1) *Crossopterygii*; (2) *Chondrostei*; (3) *Protospondyli*; (4) *Halecostomi*.

Order 1. CROSSOPTERYGII. Fringe-finned Ganoids.

Notochord persistent or vertebral rings ossified. Tail diphycercal, hetero-diphycercal, or gephyrocercal. Clavicle present. Paired fins with a scaly axis fringed on both sides by dermal rays. Branchiostegal apparatus between the rami of the mandible consisting of a pair of large jugular plates, these in many Palaeozoic genera flanked by a series of small lateral jugulars and an anterior median plate. Ganoid scales rhombic or cycloidal, completely covering the trunk and tail; outer layer consisting of cosmine.

Of all fishes, the Palaeozoic *Crossopterygii* most nearly resemble the earliest *Amphibia* (or *Stegocephali*), which were in part contemporaneous with them. The arrangement of the head bones corresponds very closely, and the complex structure of the mandible is almost the same in the two groups. The peculiar structure of the conical teeth, with a more or less complex folding of the walls of dentine, is also very similar; and there are enlarged teeth on the vomerine bones in each. Some of the *Crossopterygii*, such as *Osteolepis* and *Diplopterus*, exhibit a pineal foramen, like nearly all *Stegocephali*. A few genera of the *Rhizodontidae* and *Coelacanthidae* also agree with the *Stegocephali* in having sclerotic plates round the eye.

The *Crossopterygii* were divided by Cope into four Sub-Orders according to the condition of the median fins. The *Rhipidistia*, with a simple axonost and few baseosts in each dorsal and anal fin, include the *Osteolepidae*, *Rhizodontidae*, and *Holoptychiidae*, perhaps also the *Urostheneidae*. The *Actinistia*, with anterior dorsal fin lacking baseosts, are the *Coelacanthidae*. The *Haplistia*, with axonosts numerous and not fused, may perhaps be represented by the *Tarrasiidae*. The *Cladistia*, or *Polypteridae*, may not be closely related to the other families; their scales have a thick layer of ganoine covering the cosmine, as in the Chondrostean *Palaeoniscidae*. They are separated by Stensiö as *Brachiopterygii*.

In the skull of the Rhipidistian and Actinistian *Crossopterygii*, the basicranial axis is unossified for a short space between the basioccipital and basisphenoid bones, and the cranial roof exhibits a loose transverse suture above this region. The posterior and anterior halves of the skull would therefore be slightly movable on each other.

Family 1. **Osteolepidae.**[1]

Body slender, with rhombic ganoid scales covered with cosmine. Teeth conical, only externally folded at the base. Lateral jugular plates present. Ring vertebrae at least in the caudal region. Paired fins with a short, obtuse lobe. Two dorsal fins and one anal fin, each supported by a single axonost and a row of baseosts. Tail heterocercal or diphycercal. Devonian, Carboniferous, and Lower Permian.

Osteolepis Ag. (*Tripterus, Triplopterus* M'Coy) (Fig. 170). Cranial roof bones in advance of the parietals fused into a continuous shield, pierced by a median frontal (pineal) foramen. Internal nares. An anterior median jugular plate. Teeth round in section. First dorsal fin in front of the pelvic pair. Scales smooth and punctate. *O. macrolepidotus* Ag. (Fig. 170) and *O. microlepidotus* Pander. Middle Old Red Sandstone; Scotland. Scales also in Devonian of Granite Harbour, Antarctica.

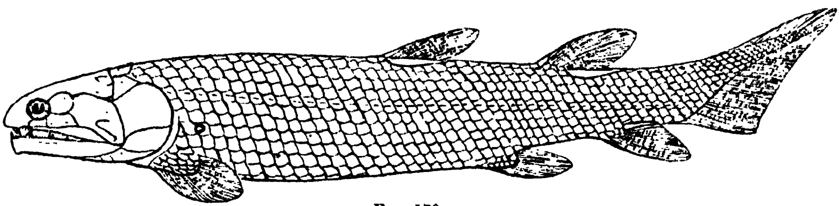


FIG. 170.
Osteolepis macrolepidotus Ag. Restoration by Traquair, about 1/2 nat. size. Middle Old Red Sandstone; Scotland.

Thursius Traq. As *Osteolepis*, but first dorsal opposite pelvic fins. Middle Old Red Sandstone; Scotland.

Diplopterus Ag. Middle Old Red Sandstone; Scotland. Probably also in W. Norway.

Megalichthys Ag. (*Centrodus* M'Coy; *Parabatrachus* Owen; *Rhomboptychius* Young; *Ectosteorhachis* Cope). Cranial roof bones in advance of the parietals rarely fused into a continuous shield, without a median frontal foramen. Teeth round in section. First dorsal fin nearly opposite the pelvic pair. Scales smooth and punctate. Carboniferous of Great Britain, Ireland, N. France, and North America. Lower Permian of Texas. *M. hibberti* Ag., the best known British species from the Coal Measures.

FIG. 171.
Glyptopomus kinnairdi Huxley. Scale, enlarged. Upper Old Red Sandstone; Dura Den, Fifeshire (after Huxley).

Glyptopomus Ag. (*Glyptolaemus* Huxley) (Fig. 171). Bones of cranial roof not fused together; a median frontal (pineal) foramen. External bones and scales ornamented with irregular reticulating rugae or fused series of tubercles. Upper Old Red Sandstone; Scotland, possibly also Belgium and Pennsylvania.

Family 2. **Rhizodontidae.**[2]

Body covered with rather thin, imbricating, cycloidal ganoid scales. Teeth few and conical, with a well-defined pulp-cavity, the wall of which is radiately folded

[1] *Goodrich, E. S.*, Head of *Osteolepis*. Journ. Linn. Soc.—Zool., vol. xxxiv., p. 181, 1919.—*Watson, D. M. S.*, Internal Ear of *Osteolepis*. Journ. of Anatomy, vol. lix., p. 385, 1925.—The Evolution and Origin of the Amphibia. Phil. Trans. Roy. Soc., vol. 214B, no. vi., 1926.

[2] *Chabakov, A. W.*, Crossoptérygiens du Carbonifère russe [in Russian]. Bull. Comité Géol. Leningrad, vol. xlvi., p. 299, 1927.—*Traquair, R. H.*, Cranial Osteology of *Rhizodopsis*. Trans. Roy. Soc. Edinb., vol. xxx., p. 167, 1881.

in the lower part of the crown (rhizodont). Enlarged laniary teeth on several separate inner bones in lower jaw. Lateral and a median jugular plate present. Sometimes bony ring vertebrae. Paired fins with a short, obtuse lobe. Two dorsal fins and one anal fin, each supported by a single axonost and a row of baseosts. Tail diphycercal or heterocercal. Devonian and Carboniferous.

Rhizodus Owen (*Megalichthys* Ag. p.p.) (Fig. 172). Very large, incompletely known fishes with rough, rugose cycloidal scales. Clavicle with a long upwardly directed process. Teeth smooth, compressed to a sharp edge in front and behind. *R. hibberti* Ag., and *R. ornatus* Traq., from Lower Carboniferous, Scotland and Northumberland. Allied species in Coal Measures of North America.

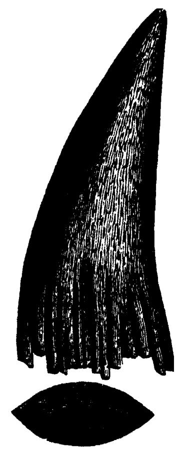


FIG. 172.
Rhizodus hibberti Ag. Tooth, 1/2 nat. size. Lower Carboniferous; Edinburgh.

Strepsodus Young (*Dendroptychius* Young; *Archichthys* Hanc. and Atth.). Large and medium-sized fishes with slender and somewhat curved teeth, which are not compressed to sharp edges. Clavicle with a long upwardly directed process. Vertebral centra are thin discs, pierced by notochord. *S. sauroides* Binney sp., from Coal Measures of England, Scotland, Ireland, N. France, and Silesia. *S. siberiacus* Chabakov, from Lower Carboniferous, Govt. Jenissei, Siberia. *S. decipiens* A. S. Woodw., from Carboniferous, Mansfield, Victoria, Australia. Other species from Lower Carboniferous of Scotland, Ireland, and Nova Scotia.

Rhizodopsis Young (*Dittodus*, *Ganolodus*, *Characodus*, *Gastrodus* Owen) (Fig. 173). Scales oval, with an extremely thin layer of cosmine. Teeth round in section, smooth. Vertebral axis with ring vertebrae. The small type species represented by fine examples in the English Coal Measures. Fragments in the Coal Measures of N. France, Silesia, S. Russia, Nova Scotia, and Illinois.

Tristichopterus Egerton. Teeth round in section. Ring vertebrae. Dorsal fins directly opposite pelvic and anal fins. Tail almost heterocercal and truncated. Scales with rugose cosmine. *T. alatus* Eg. Middle Old Red Sandstone; Scotland. Probably also in W. Norway.

Eusthenopteron Whiteaves (Fig. 30 *B*, p. 19).[1] As *Tristichopterus*, but teeth laterally compressed and tail diphycercal. Sclerotic plates round eye. *E. foordi* Whit. Upper Devonian; Scaumenac Bay, P.Q., Canada.

Gyroptychius M'Coy. Middle Old Red Sandstone; Scotland.

Cricodus Ag. (*Polyplocodus* Pander). Upper Old Red Sandstone; Scotland, Latvia, Russia, and Belgium.

Sauripterus Hall (Fig. 30 *A*, p. 19). Pectoral fin known. Upper Devonian; Pennsylvania.

Dictyonosteus Stensiö.[2] Known by skull lacking occipital and auditory

[1] *Aldinger, H.*, Über einige Besonderheiten im Schädeldach von *Eusthenopteron foordi* Wh. Centralbl. f. Min., etc., Abt. B, p. 300, 1931.—*Bryant, W. L.*, Structure of *Eusthenopteron*. Bull. Buffalo Soc. Nat. Sci., vol. xiii., p. 1, 1919.—*Hussakof, L.*, Devonic Fishes from Scaumenac Bay. New York State Mus. Bull. 158, p. 131, 1912.—*Stensiö, E. A.*, Caudal Fin of *Eusthenopteron*. Archiv för Zoologi, vol. 17B, no. 11, 1925.

[2] *Stensiö, E. A.*, Crossopterygian Fish from Upper Devonian of Spitzbergen. Bull. Geol. Inst. Upsala, vol. xvi., p. 115, 1918.—Notes on Certain Crossopterygians. Proc. Zool. Soc., 1922, p. 1241.

region, displaying many anatomical characters. *D. arcticus* Stensiö. Upper Devonian; Mimer Valley, Spitzbergen.

Euporosteus Jaekel. Middle Devonian; Eifel.

? *Devonosteus* Jaekel. Upper Devonian; Wildungen.

? *Rhomboderma* Chabakov. Scale from Lower Carboniferous, Ural, Russia.

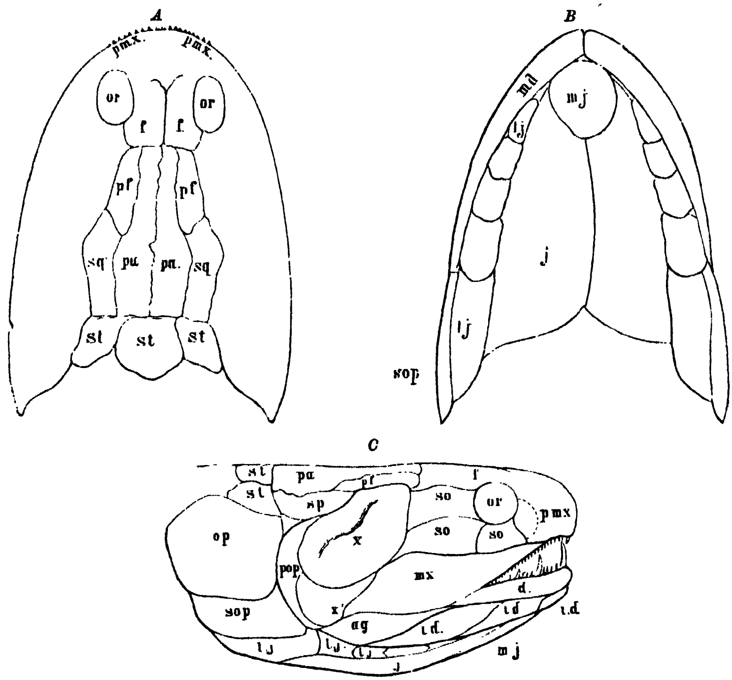


FIG. 178.

Rhizodopsis sauroides Williamson sp. Outline restorations of head and opercular apparatus from the upper (*A*), lower (*B*), and lateral (*C*) aspects, about 1/2 nat. size. Upper Carboniferous; Staffordshire. *ag*, angular; *d*, dentary; *f*, frontal; *id*, infradentary; *j*, principal jugular; *lj*, lateral jugular; *mj*, median jugular; *md*, mandible; *mx*, maxilla; *op*, operculum; *or*, orbit; *pa*, parietal; *pf*, postfrontal; *pmx*, premaxilla; *pop*, preoperculum; *so*, suborbital; *sop*, suboperculum; *sq*, squamosal; *st*, supratemporal; *x*, *x'*, cheek-plates (after Traquair). This is the original nomenclature of Traquair and Zittel.

Family 3. **Urostheneidae.**[1]

Imperfectly known, but paired fins probably with a very short, obtuse lobe. One large dorsal fin more or less opposed to the anal fin. Tail heterocercal, without fin rays on its upper margin. No ossified vertebrae. Body covered with thin, imbricating, cycloidal ganoid scales. Permian.

Urosthenes Dana. A stout fish with maximum depth of trunk at the origin of the dorsal and anal fins, which are directly opposed, longer than deep, gently rounded, each on a low lobe. Caudal fin truncated behind. All the fin rays slightly spaced, stout but most of them closely articulated and finely divided distally. Scales ornamented with sharp, delicate ridges in chevron pattern, the apex backwards. *U. australis* Dana and *U. latus* A. S. Woodw., about 40 cm. long. Newcastle Coal Measures; New South Wales.

[1] *Woodward, A. S.*, On *Urosthenes*. Ann. Mag. Nat. Hist. [10], vol. viii., p. 365, 1931.

Family 4. **Holoptychiidae.**

Body covered with imbricating, cycloidal ganoid scales. Teeth numerous, solid, acutely conical, arranged on the border of the jaws; enlarged laniary teeth in a second inner series on several separate bones in lower jaw. The teeth distinguished by a very complicated, meandering, folded structure (dendrodont). Lateral jugular plates present. No ossified vertebrae. Pectoral fins acutely lobate. Two dorsal fins and one anal fin, each borne by a single distally expanded axonost, followed by one or two rows of short baseosts, which support the very numerous, fine, dermal fin rays. Tail heterocercal. Devonian.

Holoptychius Ag. (*Glyptolepis, Platygnathus* Ag.) (Figs. 7, 174-176). Body rotund, the cycloidal scales large and thick, ornamented with irregular

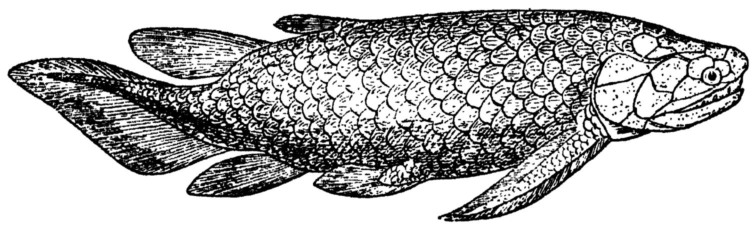


Fig. 174.
Holoptychius flemingi Ag. Restoration by Traquair, about $^1/_8$ nat. size. Upper Old Red Sandstone; Scotland.

longitudinal wrinkles or ridges of cosmine, which are partly subdivided into tubercles. Head depressed, the bones superficially granulated; teeth com-

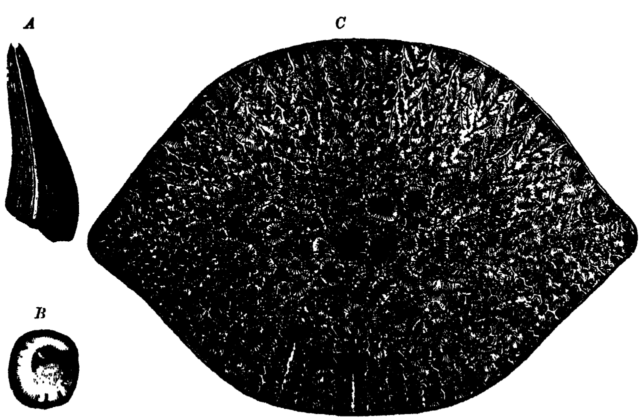


Fig. 175.
Dendrodus biporcatus Ag. Tooth in side view (*A*), and from below (*B*), nat. size, and transverse section of the same (*C*), highly magnified (after Pander).

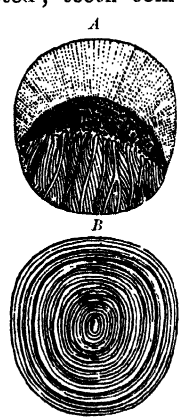


Fig. 176.
Scale of *Holoptychius* (*Glyptolepis*). Outer (*A*), and inner (*B*) aspect. Old Red Sandstone; Wik, Russia. Nat. size (after Pander).

pressed to a pair of sharp edges at least near the apex. Middle and Upper Old Red Sandstone of Scotland, England, and Ireland, and the Devonian of Latvia, Russia, Bohemia, Belgium, the Eifel, the United States, Canada,

Greenland, Australia, and Antarctica. Some species over one metre long. *H. nobilissimus* and *H. flemingi* Ag. (Fig. 174) are well preserved in the Upper Old Red Sandstone of Scotland. Detached teeth have been described as *Dendrodus* Owen[1] (Fig. 175); *Lamnodus* Ag.; and *Apedodus* Leidy.

Family 5. **Coelacanthidae.**[2]

Body covered with imbricating, thin cycloidal ganoid scales. Teeth small and conical, more or less clustered. Only one opercular bone on each side and a pair of jugular plates; several membrane bones in mandible. No ossified vertebrae. Arches, spinous processes, and supports of caudal fin superficially ossified. Air bladder ossified. Paired fins with a short, obtuse lobe. Each of the two dorsal fins and the anal fin supported by a simple, usually proximally forked plate, which in the anterior dorsal is in direct contact with the dermal rays. Caudal fin diphycercal, borne above and below by simple supports, one to each ray, and usually terminating in a small projecting tufted fin. Upper Devonian to Upper Cretaceous.

The short obtuse lobe of the pectoral fin in the *Coelacanthidae*, so far as known, is supported by from four to six partially ossified rods which radiate from a centre on the pectoral arch.[3]

Diplocercides Stensiö (*ex* Jaekel MS.). Structure of skull well shown. *D. kayseri* Koenen sp., and *D. jaekeli* Stensiö, from Upper Devonian, Wildungen, Germany.

? *Coelacanthopsis* Traquair.[4] Lower Carboniferous (Calciferous Sandstones); Fifeshire.

? *Palaeophichthys* Eastman. Coal Measures; Mazon Creek, Illinois.

Coelacanthus Ag. (*Hoplopygus* Ag.; *Conchiopsis* Cope; *Rhabdoderma* Reis). Teeth absent on the margin of the jaws, but a few hollow, conical teeth within. Supplementary caudal fin prominent. External bones and scales ornamented with series of tubercles or fine ridges of ganoine; fin rays not denticulated. *C. elegans* Newb., from Coal Measures of Ohio, Britain, Belgium, N. France, and S. Russia. Several other species, not more than 50 cm. long, from Carboniferous and Permian of England, Scotland, Germany (Kupferschiefer), and North America. Also Permian or Trias, Madagascar; Lower Triassic, Banff, Alberta, Canada; and Beaufort Beds, Orange River Colony, South Africa. *C. lunzensis* Teller, from Upper Trias, Raibl, Carinthia.

Graphiurus Kner; *Heptanema* Bellotti. Trias of Raibl and Perledo.

Diplurus Newb. Trias; New Jersey and Connecticut.

Wimania, Sassenia, Axelia, Mylacanthus, Scleracanthus Stensiö. Trias of Spitzbergen.

Undina Münster (*Holophagus* Egerton) (Fig. 177). Supplementary caudal fin prominent. All the fin rays robust, broad, and closely articulated distally; the anterior rays of the first dorsal and caudal fins denticulated or tuber-

[1] *Gross, W.*, Geol. u. Palaeont. Abhandl., n.f., vol. xviii., p. 139, 1930.

[2] *Huxley, T. H.*, Illustrations of the Structure of the Crossopterygian Ganoids. Mem. Geol. Surv., dec. xii., 1866.—*Reis, O.*, Die Coelacanthinen. Palaeontogr., vol. xxxv., p. 1, 1888; also Geogn. Jahresh., München, 1892, and Jahrb. k. k. geol. Reichsanst. Wien, vol. 50, p. 187, 1900.—*Stensiö, E. A.*, Coelacanthiden aus dem Oberdevon von Wildungen. Palaeont. Zeitschr., vol. iv., p. 167, 1922.—*Watson, D. M. S.*, Coelacanth Fish. Ann. Mag. Nat. Hist. [9], vol. viii., p. 320, 1921.—Reproduction of the Coelacanth Fish, *Undina*. Proc. Zool. Soc., 1927, p. 453.

[3] *Woodward, A. S.*, Mem. Geol. Surv. N.S. Wales, Palaeont. no. 9, p. 3, 1895; also *Wellburn, E. D.*, Geol. Mag., 1901, p. 71.

[4] *Traquair, R. H.*, Proc. Roy. Phys. Soc. Edinb., vol. xvi., p. 84, 1905.

culated. External bones and scales rugose and tuberculated. Lower Lias to Purbeckian. *U.* (*Holophagus*) *gulo* Egerton, known by nearly complete skeletons from Lower Lias, Lyme Regis. Especially fine specimens of *U. penicillata* Münst., from the Lithographic Stone of Bavaria; the same or allied species in Cerin, Ain, France, and in Lérida, Spain. A specimen from the Lithographic Stone of Solenhofen, described by Watson, seems to contain two embryos.

Libys Münst.; *Coccoderma* Quenst. Lithographic Stone (Lower Kimmeridgian); Bavaria and Würtemberg. *C. substriolatum* Huxl. sp., from Kimmeridge Clay, England.

Macropoma Ag. Maxilla, vomer, and palatine with conical teeth. Supplementary caudal fin absent. Fin rays robust and straight, not expanded

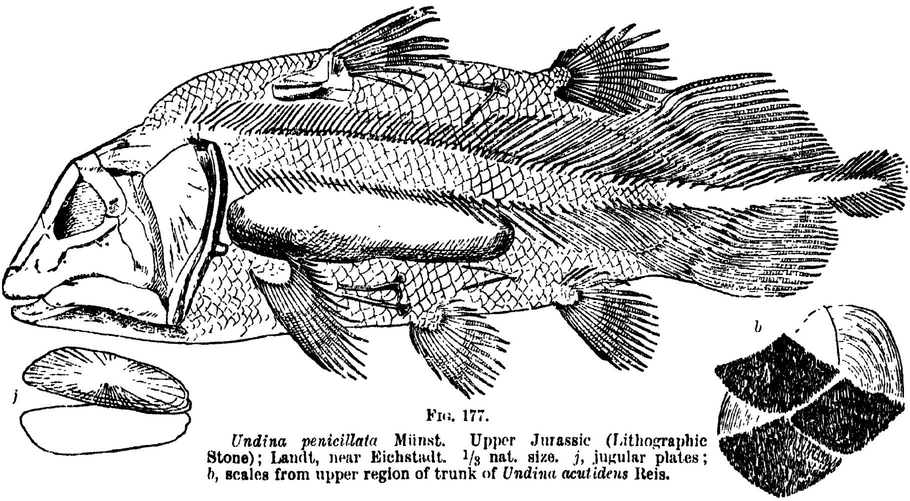


FIG. 177.

Undina penicillata Münst. Upper Jurassic (Lithographic Stone); Landt, near Eichstadt. $^1/_3$ nat. size. *j*, jugular plates; *b*, scales from upper region of trunk of *Undina acutidens* Reis.

distally, with distant articulations; a double series of small, upwardly pointing denticles on nearly all the rays of the first dorsal and caudal fins. Ornament of scales spinous. Turonian and Senonian of Europe and Lebanon. *M. mantelli* Ag., about 60 cm. long, especially well preserved in the English Chalk.

Mawsonia A. S. Woodw.[1] Much resembling *Macropoma*, but external bones without ganoine. *M. gigas* A. S. Woodw., a gigantic species with skull nearly 50 cm. in length, from the Lower Cretaceous, Bahia, Brazil.

Family 6. **Tarrasiidae.**

Body elongated, covered in the caudal region with thick small rhombic ganoid scales. Pectoral fins with a short obtuse lobe. Median fin continuous, with a regular series of supports less numerous than the fin rays. Tail diphycercal. Lower Carboniferous.

Tarrasius Traquair. Calciferous Sandstone; Eskdale, Dumfriesshire.

[1] *Woodward, A. S.*, Quart. Journ. Geol. Soc., vol. lxiii., p. 134, 1907; also *loc. cit.*, vol. lxiv., p. 358, 1908.

Family 7. **Polypteridae.**[1]

Body covered with thick, rhombic, ganoid scales. Teeth sharply conical, with simple pulp-cavity. Only a single pair of jugular plates. Vertebrae and the complete internal skeleton ossified. Pectoral fins with short, obtuse lobe, the numerous short, fan-like basalia attached to two diverging bones (propterygium and metapterygium) and a median mesopterygium. Dorsal fin single, remarkably extended, the spine-like fringed rays borne by a corresponding number of supports. Tail gephyrocercal. Tertiary and Recent.

To this family belong the two genera, *Polypterus* G. St. Hilaire (Fig. 178) and *Calamoichthys* J. A. Smith, living in the rivers and lakes of tropical Africa. Scales are known from the Eocene of Egypt.

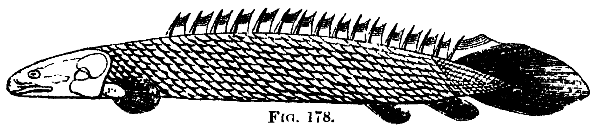


FIG. 178.

Polypterus bichir Geoffr. Recent; Upper Nile. 1/10 nat. size.

According to Goodrich this family should be placed near the *Palaeoniscidae* in the *Chondrostei*. *Polypterus* agrees with the Palaeoniscids in the structure of the scales and head bones, and in some features of the skull; its jugular plates may represent the enlarged anterior pair of branchiostegals of the Palaeoniscids; and the structure of the paired fins is actinopterygian rather than crossopterygian.

Order 2. CHONDROSTEI. Cartilaginous Ganoids.

(*Palaeopterygii* Regan.)

Notochord persistent, and endoskeleton chiefly cartilaginous; head covered with bony plates. No paired jugular plates, but usually branchiostegal rays with a median jugular plate in front. Clavicle present. Paired fins without a scaly axis, but each pelvic fin with a row of cartilaginous basal supports. A single dorsal and anal fin, with dermal rays more numerous than their supports. Caudal fin heterocercal (rarely diphycercal), and the upper lobe usually covered with rhombic scales.

In the known families of this Order the maxilla is deepened behind, and the wide preoperculum, when present, extends above this expansion on the cheek. There is no coronoid process in the mandible. In the Palaeozoic and Triassic genera the chondrocranium is more extensively ossified than in the later genera.

Family 1. **Palaeoniscidae.**[2]

Trunk elongate-fusiform; tail elongate-heterocercal. Head bones more or less enamelled; parietal and frontal bones paired. Opercular apparatus lacking only

[1] *Goodrich, E. S.*, *Polypterus* a Palaeoniscid? Palaeobiologica, vol. i., p. 87, 1928.

[2] *Lambe, L. M.*, Palaeoniscid Fishes from the Albert Shales of New Brunswick. Contrib. Canadian Palaeont., vol. iii., mem. no. 3, 1910.—*Moodie, R. L.*, Palaeoniscid Brain. Ann. Rep. Iowa Geol. Surv., 1929, vol. xxxv., p. 489, 1931.—*Stensiö, E. A.*, Triassic Fishes from Spitzbergen, pt. i., Vienna, 1921 (on this see *Allis, E. P.*, The Myodome and the Trigemino-facialis Chamber in the *Coelacanthidae* and *Palaeoniscidae*. Journal of Anatomy, vol. lvi., p. 149, 1922).—*Traquair, R. H.*, The Ganoid Fishes of the British Carboniferous Formations. Palaeont. Soc., 1877–1901.—On *Amblypterus*, *Palaeoniscus*, *Gyrolepis*, and *Pygopterus*. Quart. Journ. Geol. Soc., vol. xxxiii., p. 548, 1877.—On Eskdale Fishes. Trans. Roy. Soc. Edinb., vol. xxx., p. 15, 1881.—*Watson, D. M. S.*, Structure of Certain Palaeoniscids. Proc. Zool. Soc., 1925, p. 815; also *loc. cit.*, 1928, p. 49.—*White, E. I.*, Fish-fauna of the Cementstones of Foulden, Berwickshire. Trans. Roy. Soc. Edinb., vol. lv., p. 255, 1927.

interoperculum. Teeth slender, conical or styliform; a marginal series of small teeth, with larger teeth within. Scales ganoid, rhombic in shape, rarely cycloid on the trunk. Devonian to Wealden.

Stegotrachelus A. S. Woodw. and White. Head short and deep; mandibular suspensorium slightly oblique. Branchiostegal rays relatively large and few. Pelvic fins short-based; dorsal and anal fins opposed; caudal fin forked. Scales small, rhombic, not many deeper than long, all ornamented with horizontal ridges and intercalated pittings. A series of enlarged dorsal ridge-scales. *S. finlayi* Woodw. and White. Middle Old Red Sandstone; Shetland. Small Palaeoniscids with similar scales occur also in the Upper Devonian of New York State (*Palaeoniscus devonicus* Clarke), and of Granite Harbour, Antarctica.

Cheirolepis Ag. Mouth large and mandibular suspensorium oblique. Pelvic fins long-based. Dorsal fin remote, arising behind the origin of the anal fin. Scales very small, rhombic, or almost square. *C. cummingiae* Ag. Middle Old Red Sandstone; Scotland. *C. canadensis* Whiteaves. Upper Devonian; Scaumenac Bay, Canada.

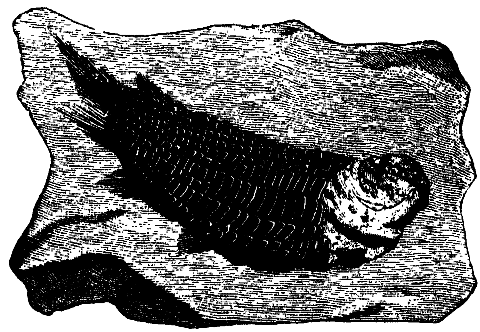


FIG. 179.
Eurylepis tuberculatus Newb. Coal Measures; Linton, Ohio. Nat. size.

Actinophorus Newberry. Upper Devonian; Ohio, U.S.A.

Canobius, Gonatodus, Drydenius Traquair. Lower Carboniferous; Scotland. *G. molyneuxi* Traq. English Coal Measures.

Fouldenia, Aetheretmon White. Lower Carboniferous (Lower Calciferous Sandstone); Foulden, Berwickshire.

Amblypterus Ag. Mouth and teeth small. Fins with delicate fulcra. Scales smooth. Several species from Lower Permian (Rothliegendes) of Rhenish Prussia, Bohemia, and France. *A. latus* Ag.; *A. duvernoyi* Ag. sp. Also from Permo-Carboniferous, Kashmir, India.

Eurylepis Newb. (Fig. 179). Small fishes with small fins, the fin rays not divided distally, and the caudal obliquely truncated. Mandibular suspensorium nearly vertical. Teeth small. Scales rugose, denticulated on the hinder border; two or more rows of scales on the flank remarkably deepened. Coal Measures; Ohio, and rarely England.

Nematoptychius Traquair; *Cycloptychius* Young. Carboniferous.

Rhadinichthys Traquair. Slender fishes, with very oblique mandibular suspensorium and small fins. Principal pectoral fin rays not articulated except at distal end; pelvic, dorsal, and anal fins short-based, the two latter more or less opposed; caudal fin deeply forked and unsymmetrical. Scales rhombic, delicately sculptured; enlarged ridge-scales in front of dorsal fin. *R. ornatissimus* Ag. sp. Lower Carboniferous; Scotland. *R. alberti* Jackson sp. Lower Carboniferous; New Brunswick. Coal Measures of England and North America. Carboniferous; Mendoza, Argentina.

Pygopterus Ag. Kupferschiefer, Germany; Marl Slate, England; Triassic, Spitzbergen.

Holurus Traquair. Fin rays articulated but not divided distally, dorsal fin extended, caudal fin obliquely truncated. Mandibular suspensorium oblique. Scales sculptured, and dorsal ridge-scales much enlarged. Lower Carboniferous; Scotland.

Dipteroma, Cosmopoma, Elaveria, Commentrya, Amblypterops, Paramblypterus, Geomichthys Sauvage.[1] Coal Measures; Commentry, France.

Palaeoniscus Blv. emend. Traquair (Fig. 180). Slender fishes, small or of moderate size. Teeth small. Fins small, the rays articulated and divided

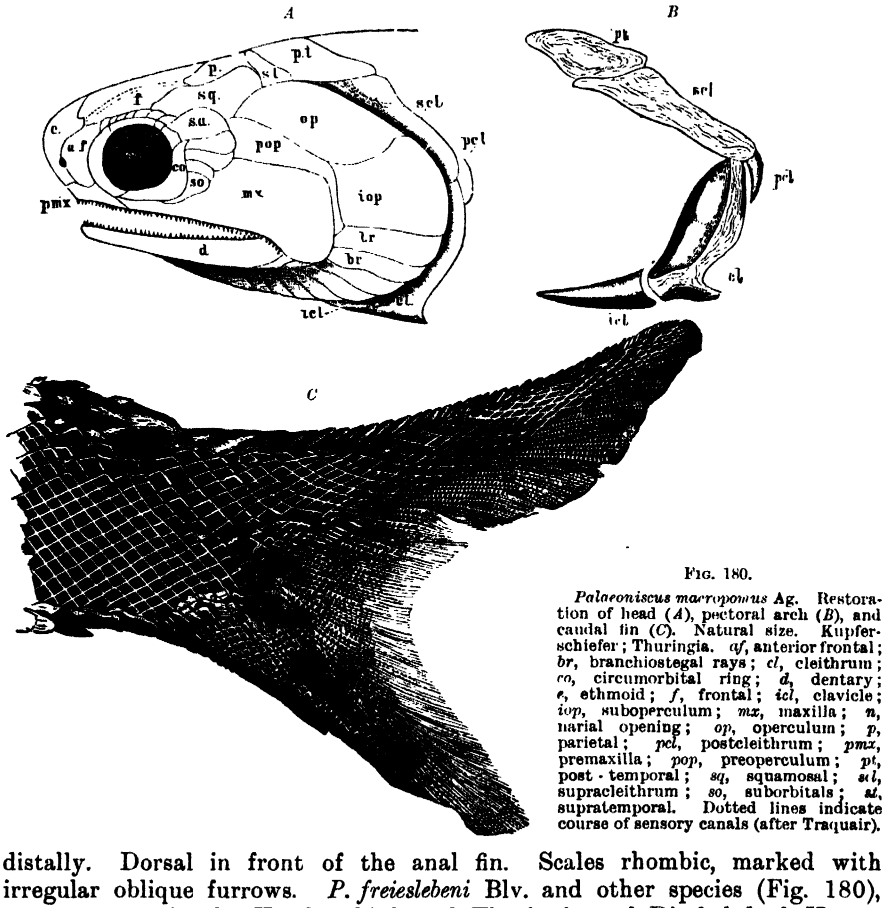


FIG. 180.

Palaeoniscus macropomus Ag. Restoration of head (*A*), pectoral arch (*B*), and caudal fin (*C*). Natural size. Kupferschiefer; Thuringia. *af*, anterior frontal; *br*, branchiostegal rays; *cl*, cleithrum; *co*, circumorbital ring; *d*, dentary; *e*, ethmoid; *f*, frontal; *icl*, clavicle; *iop*, suboperculum; *mx*, maxilla; *n*, narial opening; *op*, operculum; *p*, parietal; *pcl*, postcleithrum; *pmx*, premaxilla; *pop*, preoperculum; *pt*, post-temporal; *sq*, squamosal; *scl*, supracleithrum; *so*, suborbitals; *st*, supratemporal. Dotted lines indicate course of sensory canals (after Traquair).

distally. Dorsal in front of the anal fin. Scales rhombic, marked with irregular oblique furrows. *P. freieslebeni* Blv. and other species (Fig. 180), very common in the Kupferschiefer of Thuringia and Riechelsdorf, Hesse; also found in the Upper Permian of England, France, and Russia. Probably in the Hawkesbury Formation of New South Wales, Australia. Otoliths have been noticed by Hennig in *P. freieslebeni* from the Kupferschiefer.

Apateolepis A. S. Woodw. Fins small; no fulcra. Scales very thin, with oblique sculpturing. *A. australis* A. S. Woodw. Hawkesbury Formation; Gosford, New South Wales.

[1] *Sauvage, H. E.*, Poissons du Terrain Houiller de Commentry. Bull. Soc. Indust. Minéral. St. Étienne [3], vol. ii., p. 1, 1888.

Strepheoschema White. Unusually deep-bodied, with large ridge-scales above and below. *S. fouldenensis* White. Lower Carboniferous (Lower Calciferous Sandstones); Foulden, Berwickshire.

Elonichthys Giebel (*Rhabdolepis* Troschel; *Cosmoptychius* Traquair) (Figs. 181, 182). Fins large, with fulcra, and the rays distally divided. Dorsal in front of the anal fin. Scales rhombic, obliquely sculptured. *E. germari* Gieb., from Coal Measures of Saxony. Other species from the Carboniferous of England, Scotland, Australia, and North America; from the Lower Permian of Rhenish Prussia and Bohemia; and apparently from the Karroo Formation of the Fraserburg district, South Africa. Fragments of the same, or an allied genus, in the Permo-Carboniferous of Brazil.

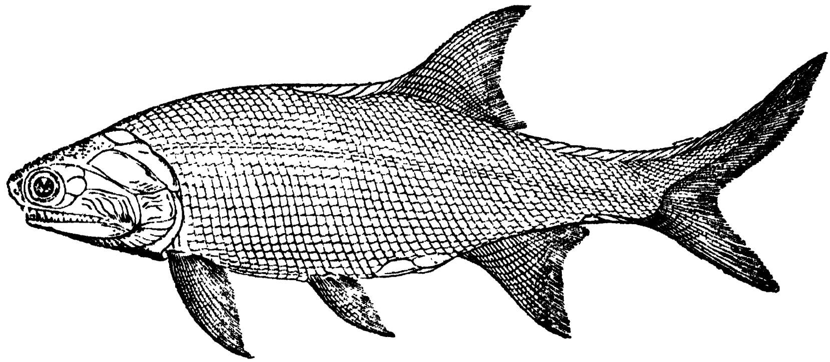


FIG. 181.
Elonichthys robisoni Hibbert sp. Restoration by Traquair, about $^2/_3$ nat. size. Lower Carboniferous; Scotland.

FIG. 182.
Elonichthys (*Cosmoptychius*) *striatus* Ag. sp. Scale from outer (*A*), and inner (*B*) aspects, three times nat. size. Lower Carboniferous; Edinburgh (after Traquair).

Acrolepis Ag. Closely resembling *Elonichthys*, but scales more deeply overlapping. *A. sedgwicki* Ag., from Upper Permian (Marl Slate of Durham and Kupferschiefer of Germany), and allied species from the Permian of Orenburg, Russia. *A. laetus* Lambe, from Lower Triassic, Banff, Alberta, Canada. Other species in Carboniferous of England, Scotland, Belgium, and Nova Scotia, and in Permo-Carboniferous of Rhodesia.

FIG. 183.
Gyrolepis ornatus Gieb. Scales enlarged. Muschelkalk; Esperstädt (after Dames).

Gyrolepis Ag. (Fig. 183). Anterior rays of pectoral fins not articulated. Operculum deep and narrow. Scales marked with irregular oblique and curved rugae. Common in the Muschelkalk and Rhaetic Bone-bed, but usually only isolated scales. *G. ? gillioti* Priem. Permian or Trias; N. Madagascar.

Birgeria Stensiö. Large fishes with low and broad head, apparently with scales only on upper caudal lobe. *B. mougeoti* Stensiö (supposed to be identical with *Saurichthys mougeoti* Ag. from Muschelkalk). Trias; Spitzbergen.

Boreosomus, *Acrorhabdus*, *Glaucolepis* Stensiö. Trias; Spitzbergen.

Urolepis Bellotti. Trias; Lombardy.

Myriolepis Egerton. Scales very small. *M. clarkei* Eg., from Trias (Hawkesbury Formation), New South Wales. *M. hibernicus* Traq., from Coal Measures of Kilkenny, Ireland.

Oxygnathus Egerton (*Thrissonotus*, *Cosmolepis* Egerton). Fins large, with small fulcra. Pectoral fin rays only articulated distally. Dorsal in front of anal fin. Scales small, but thick, obliquely sculptured. *O. ornatus* Eg. Lower Lias; Lyme Regis. *O. browni* Broom, doubtfully of this genus. Karroo Formation; South Africa.

Centrolepis, *Platysiagum* Egerton. Lower Lias; Lyme Regis.

Atherstonia A. S. Woodw.; *Dicellopygae* Brough; *Broometta* Chabakov. Trias (Karroo Formation); South Africa. *Atherstonia colcanapi* Priem. Permian or Trias; S.W. Madagascar. Other species in Hawkesbury Beds of New South Wales, and in Upper Permian of European Russia.

Namaichthys Gürich. Dwyka Formation; Ganikobis, S.W. Africa.

Coccolepis Ag. Scales thin, rounded, and very deeply overlapping; ornamented with tubercles. Fulcra minute or absent. Dorsal in front of anal fin. Small species, 6 to 14 cm. long, in the Upper Jurassic Lithographic Stone of Bavaria (*C. bucklandi* Ag.), the Purbeck Beds and Lower Lias of England, and the Wealden of Belgium and England. A larger species (*C. australis* A. S. Woodw.) in the Hawkesbury-Wianamatta Formation of New South Wales. Only known Palaeoniscid ranging above the Lias.

Cryphiolepis Traquair. Fins large, with fulcra. Scales large and thin, more or less rounded, very deeply overlapping, and externally striated. Lower Carboniferous; Scotland.

Sphaerolepis (*Trissolepis*) Fritsch; *Pyritocephalus* Fritsch. Permian; Bohemia.

Phanerosteon Traquair. Fins small, fulcra absent. Scales of flank rudimentary or absent. Lower Carboniferous; Scotland.

Carboveles White. With thin cycloid scales. Lower Carboniferous; Foulden, Berwickshire.

Elpisopholis A. S. Woodward. Fin rays finely divided distally; no fulcra; dorsal and anal fins much extended, partly opposed; caudal fin slightly forked. Greater part of trunk naked, but some thin rhombic scales in the abdominal region, and stout overlapping <-shaped scutes along the course of the lateral line. *E. dunstani* A. S. Woodw. Wianamatta Formation; St. Peter's, New South Wales.

Family 2. **Platysomidae.**[1]

Trunk deeply fusiform or irregularly rhombic and laterally compressed; tail elongate-heterocercal. Head bones enamelled; hyomandibular nearly vertical and mouth small; teeth, when present, more or less blunt, chiefly on the pterygoid and splenial bones. Opercular apparatus lacking only interoperculum. Fins usually with fulcra; pelvic fins small or absent; dorsal fin much extended. Scales rhombic, deepened on the flank, each with an inner vertical keel projecting as a peg at the upper border. Carboniferous and Permian (? also Triassic).

Eurynotus Ag. (*Plectrolepis* Ag.) (Fig. 184). Trunk deeply fusiform. Teeth short, obtusely conical to spheroidal. Pectoral fins large; dorsal fin arising opposite the pelvic pair and extending to the caudal fin; anal fin short-based.

[1] *Traquair, R. H.*, Structure and Affinities of the Platysomidae. Trans. Roy. Soc. Edinb., vol. xxix., p. 343, 1879.

E. crenatus Ag., from Lower Carboniferous, Scotland; other species from Ireland, Belgium, and Siberia.[1]

Benedenichthys Traquair [2] (*Benedenius* Traq. *nec Benedenia* Gray). Resembling *Eurynotus*, but dorsal fin less extended and ridge-scales larger. Branchiostegal rays unusually slender. *B. deneensis* van Bened. sp. Lower Carboniferous; Denée, Prov. Namur, Belgium.

Mesolepis Young; *Wardichthys* Traquair. Carboniferous; Scotland and England.

Cheirodus M'Coy (*Amphicentrum* Young; *Hemicladodus* Davis) (Fig. 185). Trunk deep, rhombic. Pectoral fins very small, pelvic fins absent. Dorsal and anal fins directly opposed, and both much extended. Teeth absent, but pterygoid and splenial with denticulated border. *C. granulosus* Young sp. (Fig. 185), from English and Scottish Coal Measures. Other species in Lower Carboniferous, England, Scotland, and Coal Measures, North America.

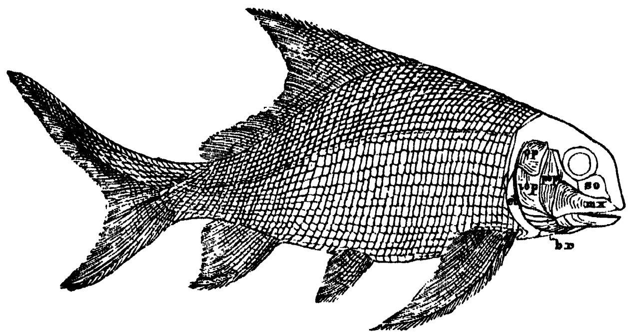


FIG. 184.

Eurynotus crenatus Ag. Restoration by Traquair, about 1/2 nat. size. Lower Carboniferous; Scotland. *br*, branchiostegal rays; *cl*, cleithrum; *iop*, suboperculum; *mx*, maxilla; *op*, operculum; *pop*, preoperculum; *so*, suborbital.

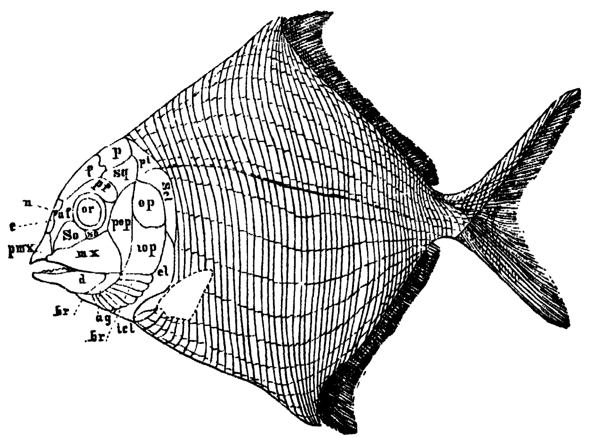


FIG. 185.

Cheirodus granulosus Young sp. Restoration by Traquair, about 1/2 nat. size. Coal Measures; North Staffordshire. Lettering as in Fig. 180.

Cheirodopsis Traquair. Lower Carboniferous; Scotland.

[1] *Chabakov, A. W.*, Poissons du genre *Eurynotus* de la série productive du bassin houiller de Kouznetz en Sibérie [in Russian]. Bull. Comité Géol. Leningrad, vol. xlvi., p. 311, 1927.

[2] *Boulenger, G. A.*, Ann. Mag. Nat. Hist. [7], vol. iv., p. 445, 1899; also *loc. cit.*, vol. x. p. 52, 1902.

Platysomus Ag. (Figs. 186, 187). Trunk deep, rhombic or discoidal. Teeth small, styliform. Pectoral and pelvic fins small, the pectorals near ventral border. Scales finely striated. *P. striatus* Ag. (Fig. 186), from Upper Permian (Marl Slate of England, Kupferschiefer of Germany). Upper and Lower Carboniferous of England and Scotland; Coal Measures of North America; Permian of Orenburg, Russia, and Texas, U.S.A.; Hawkesbury Formation of New South Wales; Lower Triassic of Spitzbergen (*P. nathorsti* Stensiö), Canada, and S. Africa.

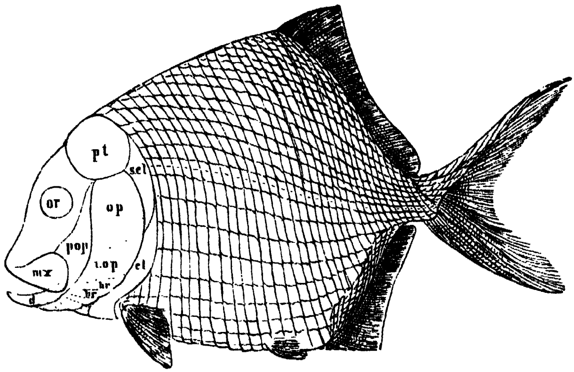


Fig. 186.
Platysomus striatus Ag. Restoration by Traquair, 1/4 nat. size. Upper Permian (Marl Slate); Durham.

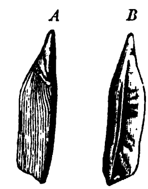


Fig. 187.
Platysomus parvulus Ag. Scale, outer (*A*), and inner (*B*) aspects, twice nat. size. Coal Measures; England.

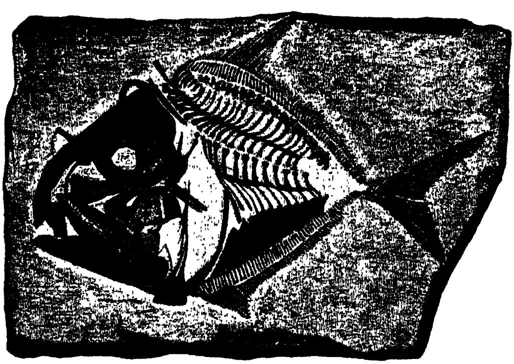


Fig. 188.
Dorypterus althausii Münst. sp. Fish, 2/3 nat. size. Kupferschiefer; Riechelsdorf.

Ecrinesomus A. S. Woodw.[1] Trunk very deeply fusiform with slender caudal pedicle. Pectoral fins large, raised on flank; no pelvic fins. Dorsal and anal fins much extended, acuminate in front. Head bones and scales finely striated. *E. dixoni* A. S. Woodw. Permian or Trias; Andogozo, Madagascar.

Caruichthys Broom. Karroo Formation; Doorn River, Cradock district, South Africa.

Globulodus Münster (*Eurysomus* Young). A single series of large, rounded, flattened pedunculated teeth on margin of jaws, smaller crushing teeth within. *G. macrurus* Ag. sp., from Upper Permian (Kupferschiefer of Germany and Marl Slate of Durham).

? *Bobasatrania* White. Permian or Trias; Madagascar.

? *Dorypterus* Germar (Fig. 188).[2] A scaleless fish, showing internal

[1] *Woodward, A. S.*, Ann. Mag. Nat. Hist. [8], vol. v., p. 1, 1910.

[2] *Gill, E. L.*, Trans. Roy. Soc. Edinb., vol. liii., no. 31, 1925.—*Weigelt, J.*, Leopoldina (Halle), vol. vi., p. 613, 1930.—*White, E. I.*, *Bobasatrania*. Ann. Mag. Nat. Hist. [10], vol. x., p. 80, 1932.

skeleton. Rare in Upper Permian (Kupferschiefer of Germany and Marl Slate of Durham).

Family 3. **Catopteridae.**

Trunk elongate or elongate-fusiform ; tail abbreviate-heterocercal. Head bones well developed, ganoid, apparently as in Palaeoniscidae*; teeth slender, conical. Dorsal fin not much extended. Scales rhombic, ganoid.* Triassic.

Dictyopyge Egerton. Teeth small. Dorsal opposite or slightly in front of the anal fin. Upper lobe of tail very short; caudal fin forked. Scales rhombic, smooth or with few oblique furrows. Species to 20 cm. long. Upper Trias of England, Ireland, Germany, Virginia (U.S.A.), and Australia. Also *D. rhenana* Deecke, from Lower Trias (Bunter), near Basle, Switzerland.

Catopterus Redfield (*Redfieldius* Hay). As *Dictyopyge*, but origin of dorsal behind that of anal fin. Fulcra fine. Trias ; North America.

Helichthys Broom ; *Daedalichthys* Brough. Karroo Formation (*Cynognathus* zone) ; South Africa.

Family 4. **Chondrosteidae.**[1]

Parietal and frontal bones paired ; a large squamosal bordering the parietals on each side. Jaws toothless, and premaxilla absent. Operculum small, suboperculum large ; a few branchiostegal rays present. Trunk naked, only the elongate upper fulcrated lobe of the tail with elongated, oat-shaped ganoid scales. Lower Jurassic.

Chondrosteus Egerton (Fig. 189). Mouth very small and inferior; jaws toothless; maxilla arched, much expanded behind and tapering in front.

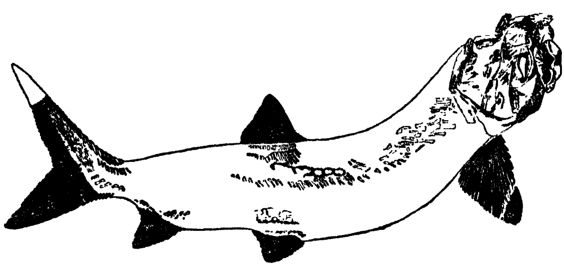


FIG. 189.
Chondrosteus acipenseroides Egerton. Lower Lias ; Lyme Regis, Dorset. $^1/_{12}$ nat. size (after A. S. Woodward).

About ten branchiostegal rays, but no jugular plate. Dorsal fin short-based, opposed to the pelvic pair. *C. acipenseroides* Eg., about a metre in length, known by nearly complete skeletons from the Lower Lias of England. *C. hindenburgi* Pomp., from Upper Lias of Holzmaden, Würtemberg.

Gyrosteus A. S. Woodward (*ex* Ag. MS.). Usually much larger than *Chondrosteus*, and the toothless maxilla expanded in its front portion for a

[1] *Hall, T. S., Psilichthys.* Proc. Roy. Soc. Vict., n.s., vol. xii., p. 147, 1900.—*Hennig, E., Chondrosteus hindenburgi* Pomp. Palaeontogr., vol. lxvii., p. 115, 1925.—*Reis, O. M., Stichopterus.* Rech. géol. et min. Chemin de Fer de Sibérie, livr. 29, p. 15. St. Petersburg, 1909.—*Traquair, R. H., Chondrosteus acipenseroides.* Geol. Mag., 1887, p. 248.—*Woodward, A. S.,* On the Palaeontology of Sturgeons. Proc. Geol. Assoc., vol. xi., p. 24, 1889 ; also Proc. Yorks. Geol. and Polyt. Soc., vol. xiii., p. 461, 1898.

palatine articulation. *G. mirabilis* A. S. Woodw. (*ex* Ag. MS.), represented by fragments in the Upper Lias of Whitby.

Psilichthys T. S. Hall. Dorsal fin behind pelvic pair. *P. selwyni* Hall. Jurassic or Triassic; Dundas county, Victoria, Australia.

Stichopterus Reis. Lower Jurassic; Siberia.

Family 5. **Acipenseridae.** Sturgeons.

Elongated fishes with a produced snout, and small toothless mouth without premaxilla. Parietal and frontal bones large, unsymmetrical, and granulated. Operculum incompletely developed, not quite covering the branchial opening; branchiostegal rays absent. Dorsal and anal fins borne by two rows of supports (axonosts and baseosts); caudal fin elongate-heterocercal, the large upper lobe ridged with fulcral scales. Trunk with five longitudinal series of keeled bony plates. Tertiary and Recent.

The Sturgeons of the two living genera, *Acipenser* and *Scaphirhynchus*, inhabit the seas of the northern hemisphere, and enter the rivers of Europe, Asia, and North America. Fossil remains are rare. An Eocene species (*Acipenser toliapicus* Ag.) is represented by scutes in the London Clay of Sheppey. An Oligocene species (*A. parisiensis* Priem) occurs in the Paris Basin. Scutes and pectoral fin rays are also known from Upper Eocene and later deposits in Europe, and from the Miocene of Virginia, U.S.A.

Family 6. **Polyodontidae.** Paddle-fishes.

Snout very long and spatulate. Parietal and frontal bones paired. Mouth large, with minute teeth in both jaws; no premaxilla. Branchiostegal rays absent. Scales rudimentary or absent, except on the sides of the upper caudal lobe, which is elongate and ridged with large fulcral scales. Cretaceous (?) or Eocene to Recent.

Crossopholis Cope. Rostrum covered with small stellate bones. Scales of trunk small, thin, and separated; each being a grooved disc with posterior denticulations like a fringe. *C. magnicaudatus* Cope. Eocene (Green River Shales); Wyoming.

Pholidurus A. S. Woodw. Known by caudal ridge-scales only, from the Upper Chalk, Kent.

Polyodon (*Spatularia*) living in the Mississippi, *Psephurus* in Chinese rivers.

Family 7. **Belonorhynchidae.**[1]

Slender fishes with a much elongated, pointed snout. Mouth very large, and jaws with numerous conical teeth of different sizes. Opercular apparatus reduced, without branchiostegal rays. Cleithrum fused with clavicle. Fin fulcra minute or absent; dorsal and anal fins small and remote; caudal fin diphycercal. Trunk with four longitudinal rows of small, keeled, scale-like plates. Triassic and Liassic.

Belonorhynchus Bronn (*Ichthyorhynchus* Bellotti; *Giffonus* Costa; *Stylorhynchus* Martin) (Figs. 190, 191). Head and trunk excessively elongated. Jaws

[1] *Reis, O. M.*, Zur Osteologie und Systematik der Belonorhynchiden. Geogn. Jahresh., vol. iv., p. 143. München, 1891.—*Stensiö, E. A.*, Triassic Fishes from Spitzbergen, pt. ii. K. svensk. Vetensk.-Akad. Handl. [3], vol. ii., no. 1, 1925.—*Woodward, A. S.*, The Fossil Fishes of the Hawkesbury Series. Mem. Geol. Surv. N.S. Wales, Palaeont. no. 4, 1890.

approximately equal in length, and mandible remarkably deep behind. Head bones externally ornamented with striae, rugae, or reticulations. The remote

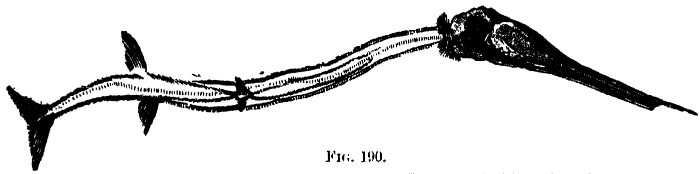


FIG. 190.
Belonorhynchus striolatus Bronn. Keuper; Raibl, Carinthia. Nat. size.

dorsal and anal fins opposed to each other; the diphycercal caudal fin truncated at its hinder margin. Of the four series of imbricating keeled

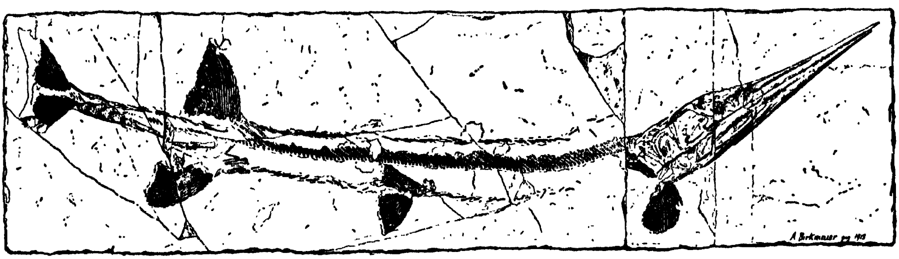


FIG. 191.
Belonorhynchus krambergeri Schlosser sp. Upper Trias; Adnet, near Salzburg. 1/8 nat. size.

dermal scutes one extends along the back, another along the ventral border, and the other two smaller series along the flanks. The ventral scutes form a ring round the region of the anus. *Belonorhynchus* occurs in the Trias of the Alps (Raibl, Perledo, Seefeld), Canada (Alberta), Spitzbergen, and Australia (Hawkesbury Formation). The teeth, jaws, and skulls from the Muschelkalk, Keuper, and Rhaetic, described under the name of *Saurichthys* Ag. (Fig. 192), may belong to *Belonorhynchus*.

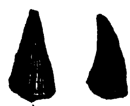


FIG. 192.
Saurichthys acuminatus Ag. Tooth, nat. size. Rhaetic; Kemnath, Würtemberg.

Acidorhynchus Stensiö (*Saurorhynchus* Reis *nec* Münster). Ganoine-covering of external bones less than in *Belonorhynchus*, and opercular bones relatively smaller. *A. acutus* Ag. sp. and other species from Lias of England and Germany.

Family 8. **Pholidopleuridae.**[1]

Trunk elongate to fusiform, and snout very short; teeth minute. Vertebral rings present. Fin fulcra reduced or absent; dorsal and anal fins small and usually remote; caudal fin diphycercal. Scales rhombic and in regular close series. Triassic.

Pholidopleurus Bronn (Fig. 193). Trunk slender. Maxilla deepened behind. Scales smooth, one series very deep on the flank, those on the back and ventral region wider than deep. Pelvic fins absent. Dorsal and anal fins delicate, elongated, and low, directly opposed on the hinder part of the

[1] *Wade, R. T.*, Preliminary Note on *Macroaethes brookvalei*, representing a new Chondrostean Family, the *Pholidopleuridae*. Ann. Mag. Nat. Hist. [10], vol. ix., p. 473, 1932.

caudal region. Caudal fin externally homocercal, slightly forked. Upper Trias; Raibl, Carinthia.

Peltopleurus Kner. Much resembling *Pholidopleurus*, but pelvic fins present and dorsal in advance of anal fin. Upper Trias; Raibl, Carinthia; Besano, Lombardy; Giffoni, Salerno; Seefeld, Tyrol; Kilindi, Congo Free State.

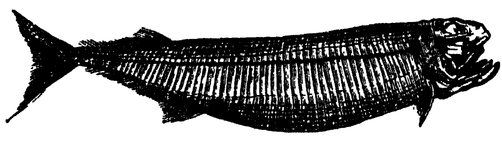


FIG. 193.
Pholidopleurus typus Bronn. Keuper; Raibl, Carinthia. $^2/_3$ nat. size (after Kner).

Macroaethes Wade. Trunk elongate, with remote dorsal and anal fins which are extended and directly opposed. Pelvic fins small and remote. Caudal fin forked. The regular squamation is thin and thus allows the supports of the dorsal and anal fins to be observed. Some of the vertebrae clearly consist of two fused rings. *M. brookvalei* Wade, sometimes 30 cm. long. Hawkesbury Sandstone; Brookvale, New South Wales.

Order 3. PROTOSPONDYLI.[1]

Notochord persistent, or vertebrae in various degrees of ossification. Head covered with bony plates. Premaxilla firmly articulated with cranium. Mandibular ramus complex. Branchiostegal rays, usually with a median jugular plate in front. At least one series of postorbitals (suborbitals) on the cheek between the orbit and preoperculum. No clavicle (except an occasional rudiment). Unpaired, and usually also paired fins fringed with fulcra; supports of dorsal and anal fins equal in number to the dermal rays. Caudal fin hemi-heterocercal.

In all except some of the earliest members of this Order, the preoperculum tapers upwards and is more or less overlapped by the suborbitals. A supramaxilla usually borders the hinder part of the maxilla. There is a coronoid process in the mandible. A rudiment of the clavicle sometimes occurs.

[1] *Alessandri, G. de*, Pesci triasici della Lombardia. Mem. Soc. Ital. Sci. Nat., vol. vii., fasc. i., 1910.—*Bassani F.*, and *D'Erasmo, G.*, Ittiofauna del Cretacico di Capo d' Orlando. Mem. Soc. Ital. Sci. Roma [3], vol. xvii., p. 1, 1912.—*Bassani, F.*, Ittiofauna della Dolomia di Giffoni. Palaeont. Ital., vol. i., 1895.—*Dames, W.*, Ganoiden des deutschen Muschelkalks. Palaeont. Abhandl., vol. iv., p. 135, 1888.—*Eastman, C. R.*, Fossil Fishes from Lithographic Stone of Cerin, France. Mem. Carnegie Mus., vol. vi., no. 6, 1914.—*Egerton, P. M. G.*, Figures and Descriptions of British Organic Remains. Mem. Geol. Surv., dec. vi., viii., ix., xiii., 1852–72. —*Gregory, W. K.*, A Jurassic Fish Fauna from Western Cuba, with an Arrangement of the Families of Holostean Ganoid Fishes. Bull. Amer. Mus. Nat. Hist., vol. xlviii., p. 223, 1923.—*Heineke, E.*, Die Ganoiden und Teleostier des lithographischen Schiefers von Nusplingen. Palaeont. Abhandl., n.f. vol. viii., pt. 3, 1907.—*Kner, R.*, Die Fische der bituminösen Schiefer von Raibl in Kärnthen. Sitzungsb. k. Akad. Wiss. Wien, math.-naturw. Cl. vol. liii., 1866; and Nachtrag, *ibid* vol. lv., 1867.—Die fossilen Fische der Asphaltschiefer von Seefeld in Tyrol. *Ibid.* vol. liv., 1866; and Nachtrag, *ibid.*, vol. lvi., 1867.—*Kramberger, K. Gorganovic*, Die obertriadische Fischfauna von Hallein in Salzburg. Beitr. Paläont. u. Geol. Österr.-Ungarns, vol. xviii., p. 193, 1905.—*Regan, C. T.*, Skeleton of *Lepidosteus*, with Remarks on the Origin and Evolution of the Lower Neopterygian Fishes. Proc. Zool. Soc., 1923, p. 445.—*Sauvage, H. E.*, Sobre los peces de la Caliza litográfica de Lérida. Mem. R. Acad. Cienc. Barcelona, vol. iv., no. 35, 1903.—*Stolley, E.*, Ganoiden des deutschen Muschelkalks. Palaeontographica, vol. lxiii., p. 25, 1920.—*Traquair, R. H.*, Les Poissons wealdiens de Bernissart. Mém. Mus. Roy. d'Hist. Nat. Belg., vol. vi., 1911.—*Vetter, B.*, Die Fische aus dem lithographischen Schiefer im Dresdener Museum. Mittheil. k. mineral.-geol. Mus. Dresden, 1881.

Family 1. Colobodontidae.[1]

Trunk fusiform, sometimes deepened. Mandibular suspensorium vertical or slightly inclined backwards; teeth styliform or tritoral, clustered on the inner bones. Differing from all other Protospondyli *in having the preoperculum extended over the cheek above the deepened hinder end of the maxilla, as in early* Chondrostei. *Notochord persistent. Scales rhombic and ganoid.* Typically Triassic.

Colobodus Ag. (*Asterodon* Münster; *Tholodus* Meyer; *Dactylolepis* Kunisch) (Fig. 194). Head bones ornamented with prominent rugae and tubercles of ganoine. Marginal teeth styliform, inner teeth hemispherical and irregularly clustered, all mammillated and marked with radiating striae. All fins with fulcra; dorsal partly opposite anal; tail slightly forked. Scales marked with oblique or horizontal ridges or plications, and usually serrated on hinder margin. *C. hogardi* Ag., *C. maximus* Dames, *C. varius* Giebel (Fig. 194), and other species in the Muschelkalk and Lettenkohle of Germany and France. Scales in Rhaetic of Aust Cliff, near Bristol. Also doubtful scales in supposed Triassic of Upper Jenissei, Siberia, and scales and teeth in the Karroo Formation of Somaliland and of Nyasaland, S.E. Africa.

Fig. 194.
Colobodus varius Giebel. Teeth and scales. Muschelkalk; Bayreuth. Nat. size.

The generic names *Nephrotus, Cenchrodus, Omphalodus, Hemilopas* Meyer, are applied to rounded teeth from the Trias.

Crenilepis Dames. Scales in German Muschelkalk. *C. bassanii* de Alessandri sp. Upper Triassic; Lombardy.

Meridensia Stensiö. Upper Triassic; Lombardy. *Meidiichthys* Brough. Karroo Formation (Upper Beaufort Beds); South Africa.

Perleidus de Alessandri. Trunk elongate-fusiform. Teeth smooth, without radiating striae. Suboperculum relatively deep. Fulcra strong. Flank scales somewhat deepened; ventral scales wider than deep. *P. altolepis* Kramb. sp., about 12 cm. long. Middle Triassic; Perledo, Lombardy. *P. woodwardi* Stensiö, about 30 cm. long. Triassic; Spitzbergen.

Dipteronotus Egerton. Keuper; Worcestershire.

Dollopterus Abel (*Dolichopterus* Compter *nec* Aymard).[2] A flying fish, with enlarged pectoral fins. Muschelkalk.

Cleithrolepis Egerton. Trunk much laterally compressed, nearly rhombic in outline. Scales narrow and very deep. Hawkesbury Formation; New South Wales. Karroo Formation (Upper Beaufort Beds); Orange River Colony, South Africa. Keuper; Coburg, Germany.

Hydropessum Broom. Upper Beaufort Beds; Orange River Colony, South Africa.

Parasemionotus Piveteau. Triassic; Madagascar.

[1] *Oertle, G. F.*, Zu *Colobodus maximus* Qu. Neues Jahrb. f. Min., etc., Beil.-Bd. 57, Abt. B, p. 243, 1927.—"*Semionotus letticus* O. Fraas." *Loc. cit.* 58, p. 309, 1927.—*Stensiö, E. A.*, Triassic Fishes from Spitzbergen, p. 253, 1921.—*Stolley E.*, Palaeontographica, vol. lxiii., p. 43, 1920.

[2] *Abel, O.*, Fossile Flugfische. Jahrb. k. k. Geol. Reichsanst. Wien, vol. 56, p. 48, 1906.—*Stolley, E.*, Palaeontographica, vol. lxiii., p. 45, 1920.

Family 2. **Semionotidae.**[1]

Trunk more or less deeply fusiform. Mandibular suspensorium vertical or inclined forwards, gape of mouth small; teeth styliform or tritoral, especially well developed on the inner bones. Not more than hemi-vertebrae or ring-vertebrae. Fin rays stout and fulcra large; dorsal fin not extending more than half length of back. Scales rhombic, except sometimes in caudal region. Upper Carboniferous or Permian to Upper Cretaceous.

? *Phanerorhynchus* E. L. Gill.[2] Coal Measures; Lancashire.

Acentrophorus Traq. Trunk fusiform. Dorsal fin short, opposite the space between the pelvic and anal fins. No enlarged ridge scales. *A. varians* Kirkby sp., and other species from Magnesian Limestone, Durham, and Kupferschiefer, Germany. *A. chicopensis* Newb. Trias; Connecticut Valley, U.S.A. Also in Trias of N. Madagascar.

Eosemionotus Stolley. *E. vogelii* Fritsch sp., from Muschelkalk.

Semionotus Ag. (*Ischypterus* Egert.; *Engycolobodus* Oertle) (Fig. 195). Trunk fusiform. Dorsal fin large and extended, its hinder part opposed to the anal fin. Dorsal series of pointed ridge scales forming a prominent crest. Fin fulcra sometimes very large. Scales and head-bones smooth or but feebly ornamented. *S. bergeri* Ag., from Keuper of Coburg and Thuringia. *S. kapffi* Fraas (Fig. 195), from Keuper, Haslach, near Stuttgart. Other species from the Bunter, Muschelkalk, Keuper, and Rhaetic of Europe, also from the Upper Karroo Formation of South Africa, Permian or Trias of N. Madagascar, the Hawkesbury Formation of New South Wales, and Trias of Connecticut Valley and New Jersey, U.S.A.

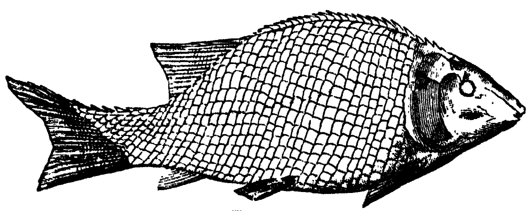


FIG. 195.
Semionotus kapffi Fraas. Keuper (Stubensandstein); Stuttgart. 2/3 nat. size (after O. Fraas).

Woodthorpea Swinnerton. *W. wilsoni* Swinn., from Keuper, Nottingham.

Aphnelepis A. S. Woodw. As *Semionotus*, but scales very thin, especially on caudal region, and no enlarged ridge scales. Hawkesbury-Wianamatta Formation (Jurassic); Talbragar, New South Wales.

Dapedius de la Beche (*Amblyurus* Ag.; *Omalopleurus* Costa; *Aechmodus* Egerton) (Figs. 196, 197). Trunk much laterally compressed, deeply fusiform or cycloidal. External bones ornamented with tubercles and ridges of ganoine. Eye surrounded by a complete ring of small quadrangular plates (*co*), behind which are from five to eight suborbitals (*so*, cheek-plates). The

[1] *Eastman, C. R.*, Triassic Fishes of New Jersey. Geol. Surv. New Jersey, Ann. Rep. 1904 (1905).—*Hennig, E.*, Neue Platte mit *Semionotus capensis*. Sitzb. Ges. naturf. Freunde, Berlin, 1915, p. 49.—*Newberry, J. S.*, Fossil Fishes and Fossil Plants of the Triassic Rocks. Monogr. U.S. Geol. Surv., vol. xiv., 1888.—*Schellwien, E.*, Über *Semionotus* Agassiz. Schriften Phys.-ökon. Gesellsch. Königsberg, vol. xlii., p. 1, 1901.—*Strüver, J.*, Fossile Fische aus dem Keupersandstein von Coburg. Zeitschr. Deutsch. Geol. Ges., vol. xvi., 1864.—*Swinnerton, H. H.*, New Catopterid Fish from the Keuper of Nottingham. Quart. Journ. Geol. Soc., vol. lxxxi., p. 87, 1925.—*Wagner, A.*, Die Griffelzähner (Stylodontes). Gelehrt. Anzeig. k. bay. Akad., vol. l., p. 81, 1860.—*Woodward, A. S.*, *Heterostrophus*. Proc. Zool. Soc., 1929, p. 561.

[2] *Gill, E. L.*, Ann. Mag. Nat. Hist. [9], vol. xi., p. 465, 1923.

supratemporal plates (*st*) also numerous. Operculum, suboperculum, and interoperculum large, arranged in an arch. Preoperculum narrow, almost or

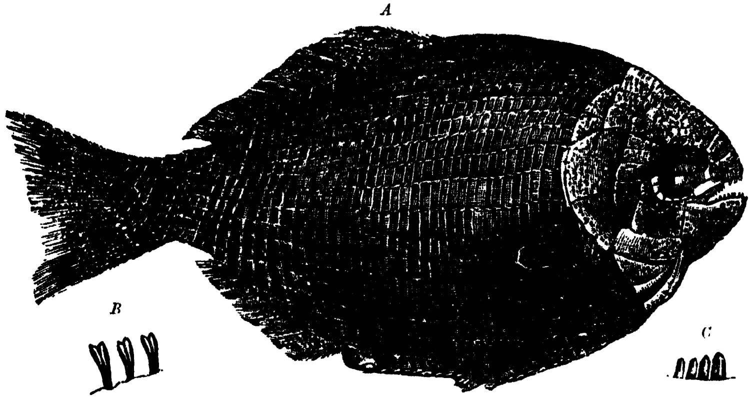


FIG. 196.
Dapedius pholidotus Ag. Upper Lias; Boll, Würtemberg. 1/2 nat. size. *B*, *C*, teeth, nat. size (after Quenstedt).

completely covered by the suborbitals. A median jugular plate in front of the laminar branchiostegal rays. Fin fulcra Λ-shaped, the two halves being fused at the apex. Pectoral and pelvic fins small; dorsal and anal fins much extended and opposed; caudal fin slightly forked. Scales on the middle of the flank deeper than broad; no prominent ridge scales; all the scales thick and enamelled, sometimes tuberculated. The earliest species in the Alpine Trias (Seefeld, St. Cassian), and in the Trias of Giffoni, Naples. Common in the Lower Lias of England and the Upper Lias of Würtemberg (Boll, Holzmaden), Bavaria (Banz), Northern France (Calvados) (*D. pholidotus* Ag.; *D. caelatus* Quenst.). Also found in the Gondwana Beds of India.

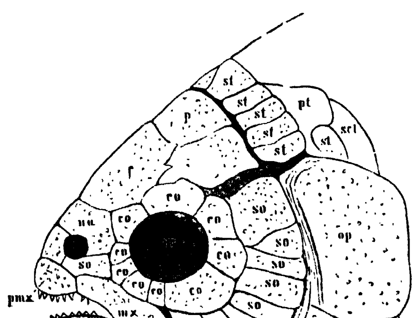


FIG. 197.
Head of *Dapedius*. *ag*, angular; *lr*, jugular plate; *br'*, branchiostegal rays; *co*, circumorbitals; *d*, dentary; *f*, frontal; *iop*, interoperculum; *mx*, maxilla; *na*, nasal; *op*, operculum; *or*, orbit; *p*, parietal; *pmx*, premaxilla; *pt*, post-temporal; *scl*, supracleithrum; *so*, suborbitals; *sop*, suboperculum; *st*, supratemporals (after Traquair).

Heterostrophus Wagner. Lithographic Stone (Upper Jurassic); Bavaria. Oxford Clay; Peterborough, England.

Aetheolepis A. S. Woodw. As *Dapedius*, but deep rhombic scales of abdominal region gradually passing into thin, deeply overlapping, oval scales on the caudal region. *A. mirabilis* A. S. W. Hawkesbury-Wianamatta Formation (Jurassic); Talbragar, New South Wales.

Tetragonolepis Bronn (*Pleurolepis* Quenst.; *Homoeolepis* Wagner). Small oval or almost cycloidal fishes, laterally compressed, with small pectoral and

pelvic fins. Dorsal and anal fins much extended. Scales deepened on the flank, their front border thickened and forming a vertical ridge. *T. semicinctus* Bronn, from Upper Lias, Würtemberg and Bavaria. Other species in the Upper Lias of England and the Gondwana Beds of the Deccan, India.

Paralepidotus Stolley. Trunk deeply fusiform. Dorsal and anal fins deep with small regular fulcra; anal about half as long as dorsal and opposite hinder part of latter. No scales much deeper than wide. *P. ornatus, latus* Ag. sp., 35 cm. to 50 cm. in length, from Keuper, Seefeld, Tyrol.

Pristisomus A. S. Woodw. As *Semionotus*, but dorsal fin short-based and opposed to anal; fin fulcra comparatively small. Hawkesbury Formation; New South Wales. Permian or Trias; N. Madagascar.

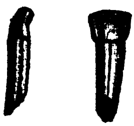


Fig. 198.

Sargodon tomicus Plien. Rhaetic; Kemnath, Würtemberg. Nat. size.

Spaniolepis Kramberger. As *Dapedius*, but scales very thin and rounded, marked with concentric lines of growth. Upper Trias; Hallein, Salzburg.

Serrolepis Quenstedt. Deep pectinated scales. *S. suevicus* Dames, from Upper Trias (Lettenkohl), Würtemberg.

Sargodon Plieninger[1] (Fig. 198). Chisel-shaped teeth with long root. Smooth, rounded, crushing teeth may belong to the same fish. Rhaetic; Würtemberg and England.

Lepidotus Ag.[2] (*Lepidosaurus* Meyer; *Scrobodus* Münster; *Sphaerodus*, p.p. Ag.; *Plesiodus* Wagner; *Prolepidotus* Michael) (Figs. 199-201). Trunk

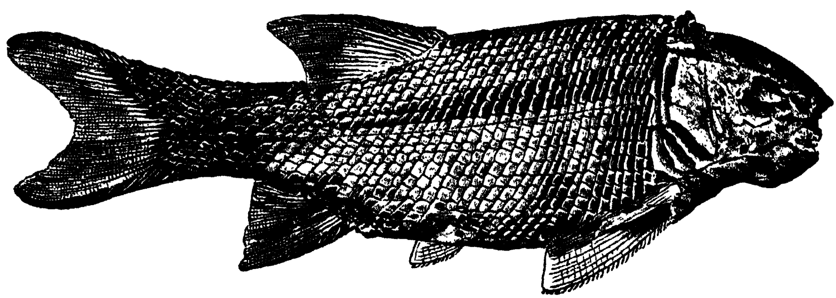


Fig. 199.

Lepidotus notopterus Ag. Upper Jurassic (Lithographic Stone); Solenhofen. 1/5 nat. size.

fusiform and only moderately compressed, covered with thick, smooth, or obliquely ridged scales, which are deeply imbricating and have the angles of the overlapped border more or less produced. Head and opercular bones more or less enamelled, smooth or tuberculated. Teeth hemispherical to obtusely conical; styliform on at least part of the edge of the mouth. Successional teeth numerous, the incipient germ lying exactly in the opposite direction to that of the functional tooth, thus making a revolution of

[1] *Peyer, B.*, Mitt. Badisch. Geol. Landesanst., vol. viii., p. 302, 1919.

[2] *Branco, W.*, Über eine neue Lepidotus-Art aus dem Wealden. Jahrb. k. preuss. geol. Landesanst., 1884, p. 181, 1885.—Beiträge zur Kenntniss der Gattung *Lepidotus*. Abh. geol. Specialk. Preussen, etc., vol. vii., pt. 4, 1887.—*Jaekel, O.*, *Lepidotus* und *Leptolepis* aus dem oberen Lias von Dobbertin, Mecklenburg. Mitteil. Mecklenburg. Geol. Landesanst., n.f. iii., heft xxxviii., p. 13, 1929.—*Priem, F.*, Étude sur le genre *Lepidotus*. Ann. Paléontologie, vol. iii., p. 1, 1908.—*Quenstedt, F. A.*, Über *Lepidotus* in Lias ε. Tübingen, 1847.—*Sauvage, H. E.*, Mémoire sur les *Lepidotus maximus* et *palliatus*. Mém. Soc. Géol. France, ser. 3, vol. i., no. 1, 1877.—Photograph of *Lepidotus* from Lithographic Stone, Bavaria, in 43 Ber. Senckenb. Naturf. Ges., p. 4, 1912. See also *Weitzel, K.*, Abhandl. Senckenb. Naturf. Ges., vol. xlii., p. 106, 1930.

180° while the root of the old tooth is absorbed and it prepares to appear (Fig. 200, *A*). Fin fulcra very large and biserial (Fig. 200, *D*), present on all

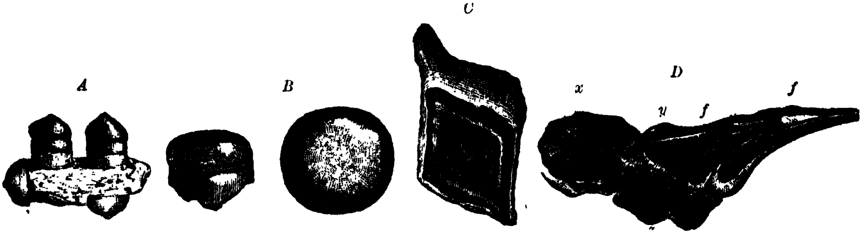


Fig. 200.

Lepidotus. *A*, fragment of jaw with successional teeth. *B*, tooth in side view and from above. *C*, scale. *D*, fulcral armature of dorsal fin. *f*, fulcra; *x*, unpaired dorsal scale; *y*, first basal scale of dorsal fin; *z*, *z'*, lateral scales. Nat. size.

the fins. Pectoral fins large; pelvic fins small; large dorsal fin opposed to the pelvic pair; caudal fin more or less forked. Ranging from the Rhaetic to the Cretaceous, some of the later species having the largest, stoutest teeth, the smallest mouth, much subdivided cheek plates and supratemporals, and well-developed ring-vertebrae. *L.* (*Prolepidotus*) *gallineki* Michael. Rhaetic; Silesia. *L. congolensis* Hussakof, from supposed Rhaetic, Lualaba, Congo Free State. The type species, *L. elvensis* Blv. sp. (Fig. 201), common in the Upper Lias of Würtemberg, Bavaria, France, and England. *L. maximus* Wagn., *L. notopterus* Ag. (Fig. 199), and other species well preserved in the Lithographic Stone (Upper Jurassic) of Germany and France. *L. minor* Ag., from Purbeck Beds. *L. mantelli* Ag., from Wealden. Also Jurassic of India, Madagascar, and Siberia, and Cretaceous of Cameroon, Tanganyika, Egypt, England, Spain, S. Dakota, and Brazil.

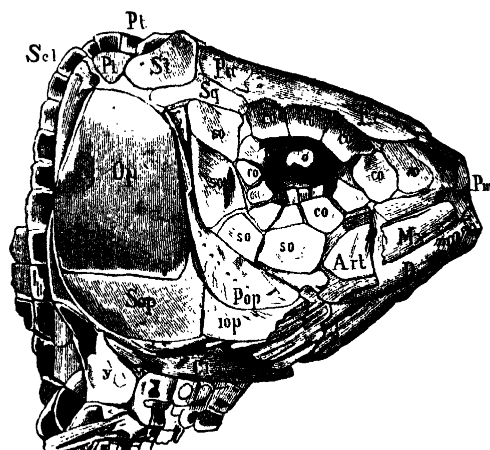


Fig. 201.

Lepidotus elvensis Blainville sp. Head. Upper Lias; Boll, Würtemberg. *art*, articulo-angular; *cl*, cleithrum; *co*, circumorbitals; *d*, dentary; *fr*, frontal; *iop*, interoperculum; *mx*, maxilla; *n*, nasal; *op*, operculum; *pa*, parietal; *pmx*, premaxilla; *pop*, preoperculum; *pt*, post-temporal; *scl*, supracleithrum; *so*, suborbitals; *sop*, suboperculum; *sq*, squamosal; *st*, supratemporal; *y*, postcleithral scale. $^1/_3$ nat. size (after Quenstedt).

Family 3. **Macrosemiidae.**

Trunk elongate or elongate-fusiform. Gape of mouth small; marginal teeth styliform, inner teeth similar or tubercular. Not more than hemi-vertebrae or ring-vertebrae. Fin rays stout and fulcra variable; dorsal fin much extended. Scales rhombic, with tendency to become rounded. Middle Trias to Upper Cretaceous.

Ophiopsis Ag. Trunk much elongated and slender, with a high dorsal fin extending half its length. Anal fin small. Ranging from the Muschelkalk

to the Purbeck Beds. *O. procera* Ag., and other species common in the Lithographic Stone of Bavaria.

Legnonotus Egerton. As *Ophiopsis*, but dorsal fin more extended and some flank scales deepened. *L. cothamensis* Eg. from Rhaetic, Aust Cliff, England. Other species in Upper Triassic, Hallein, Salzburg.

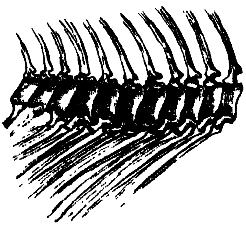


FIG. 202.
Histionotus oberndorferi Wagner. Vertebrae. Upper Jurassic (Lithographic Stone); Kelheim, Bavaria. Nat. size.

Macrepistius Cope. Lower Cretaceous; Texas.

Eusemius Vetter. Upper Jurassic; Bavaria.

Notagogus Ag. (*Blenniomoeus*, *Calignathus* Costa). Trunk elongated, with extended dorsal fin subdivided into two parts, the anterior portion with comparatively widely spaced rays, and not deeper than the posterior portion. Stout ring-vertebrae. *N. pentlandi* Ag., from Neocomian, Castellamare, near Naples. Other species in the Lithographic Stone of Bavaria and France, and Wealden of Belgium.

Propterus Ag. (*Rhynchoncodes* Costa). As *Notagogus*, but trunk deeper and anterior portion of dorsal fin deeper than posterior portion. Ring-vertebrae. Scales almost six-sided, deeper than long. Lithographic Stone of Bavaria and Lérida, Spain. Neocomian; Castellamare.

Histionotus Egerton (Fig. 202). The back of the elongated trunk elevated and sharply bent anteriorly, a single long dorsal fin extending backwards from the bend almost to the caudal fin, which is deeply forked. Uniserial fulcra on both paired and median fins. Scales of flank deeper than broad. *H. angularis* Eg., from the English Purbeck Beds. Other species from the Lithographic Stone of Bavaria and France.

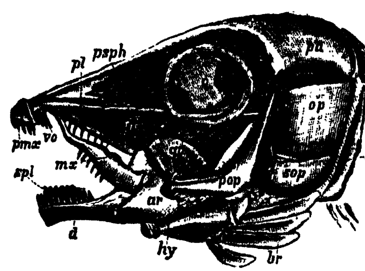


FIG. 203.
Macrosemius latiusculus Wagn. Head, nat. size. Upper Jurassic (Lithographic Stone); Kelheim. *ar*, articular; *br*, branchiostegal rays; *cl*, cleithrum; *d*, dentary; *hy*, ceratohyal; *mx*, maxilla; *o*, orbit; *op*, operculum; *pa*, parietal; *pl*, palatine; *pmx*, premaxilla; *pop*, preoperculum; *psph*, parasphenoid; *pt*, pterygoid; *qu*, quadrate; *sop*, suboperculum; *spl*, splenial; *vo*, vomer.

Macrosemius Ag. (*Disticholepis* Thioll.) (Fig. 203). Trunk elongated, and dorsal fin extending from the occiput to the caudal fin, which is rounded. No fin fulcra, but large fulcra on upper lobe of tail. Jaws and pterygoid with powerful conical or styliform teeth. Scales thin and rhombic. *M. rostratus* Ag., *M. latiusculus* Wagn. (Fig. 203), and other species in the Lithographic Stone of Bavaria and France. Doubtful jaws from Lower Jurassic (Stonesfield Slate), Oxfordshire.

Enchelyolepis A. S. Woodw. Resembling *Macrosemius* but with hemivertebrae and with very thin rounded scales. *E. andrewsi* A. S. Woodw., from English Purbeck Beds. *E. pectoralis* Sauv. sp., from Upper Portlandian, Meuse, France.

Petalopteryx Pictet (*Aphanepygus* Bassani). Upper Cretaceous; Mount Lebanon. Neocomian; Lesina, Dalmatia.

Family 4. **Pycnodontidae.**[1]

Trunk laterally compressed, very deep. No vertebrae; ribs, vertebral arches, and spines well ossified. Opercular apparatus incomplete, with much enlarged preoperculum, small operculum, and only one or two branchiostegal rays. Premaxilla with two to four prehensile teeth; maxilla deepened behind, toothless; vomerine bones fused together, usually with five longitudinal series of round or oval grinding teeth; splenial of mandible large, with coronoid process, and three, four, five, or more rows of grinding teeth; dentary small and terminal, fitting in a groove of the splenial, and bearing two to four prehensile front teeth; pterygopalatine arcade thin and toothless, its edge more or less fused with the basicranial axis. Teeth without vertical successors. Small claw-shaped pharyngeal teeth. Branchial arches with very numerous, closely arranged, bony filaments. Cleithrum broadly ovate at the lower end. Fin fulcra absent. Pelvic fins small. Dorsal and anal fins much extended. Scales deeper than long, with a thickened, ridge-like anterior margin; often reduced in the dorsal and caudal region. Upper Triassic to Upper Eocene.

Eomesodon A. S. Woodw. Abdominal region much deepened, caudal region relatively small. Jaws and teeth as in *Mesodon*, but median fins less extended. Scales complete over whole of trunk in advance of median fins. *E. hoeferi* Kramb. sp., from Upper Triassic, Hallein, Salzburg, the earliest known Pycnodont. *E. liassicus* Egert. sp., from Lower Lias, England. Numerous jaws in Lower Jurassic (*E. rugulosus* Ag. sp., etc.). *E. barnesi* A. S. Woodw., from Portlandian, Dorset.

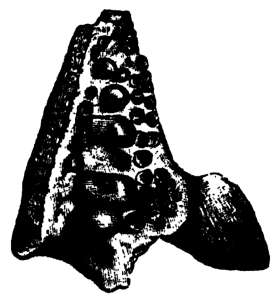


Fig. 204.
Mesodon macropterus Ag. sp. Right splenial. Upper Jurassic (Lithographic Stone); Kelheim. Nat. size.

Mesodon Wagner[2] (Fig. 204). Vomerine teeth in five longitudinal rows, the lateral pairs often irregular; splenial teeth comprising one principal series, with one or two inner series and three or more outer series usually irregularly arranged. Caudal fin rounded. Scales of dorsal half of abdominal region reduced to their riblets; no scales in caudal region, except two small rhombic scales on upper caudal lobe. *M. macropterus* Ag. sp. (Fig. 204), from Upper Jurassic (Lithographic Stone), Bavaria. *M. daviesi* A. S. Woodw. English Purbeck Beds. *M. bernissartensis* Traq. Wealden; Belgium.

Athrodon Sauvage. Splenial bone stout, meeting its fellow in a deep symphysial facet. Teeth very irregular. Kimmeridgian to Senonian. *A. douvillei* Sauv. Portlandian; Boulogne. *A. crassus* A. S. Woodw., and other species in Cambridge Greensand.

Microdon Ag. (*Polypsephus* Hay) (Figs. 205-207). Hinder half of trunk with very thin scales, which are often wanting. Vomer slender, with five rows of quadrate, smooth, and flattened teeth; between the large teeth of the middle row the smaller teeth of the two inner lateral rows are alternately pressed inwards. Splenial with one row of large, obliquely quadrate, smooth teeth, which is flanked inside by one, outside by two rows of smaller teeth. Caudal

[1] *Hennig, E.*, Gyrodus und die Organisation der Pyknodonten. Palaeontogr., vol. liii., p. 137, 1906.—Pyknodonten vom Libanon. Centralbl. f. Min., etc., 1907, p. 360.—*Woodward, A. S.*, Notes on the Pycnodont Fishes. Geol. Mag. [6], vol. iv., p. 385, 1917.

[2] *Sauvage, H. E.*, Mém. Soc. Géol. France, Paléont., no. 25, p. 13, 1902.

fin slightly forked, symmetrical. Common in the Upper Jurassic (Lithographic Stone) of Bavaria and France, and in the Purbeck Beds of England (*M.*

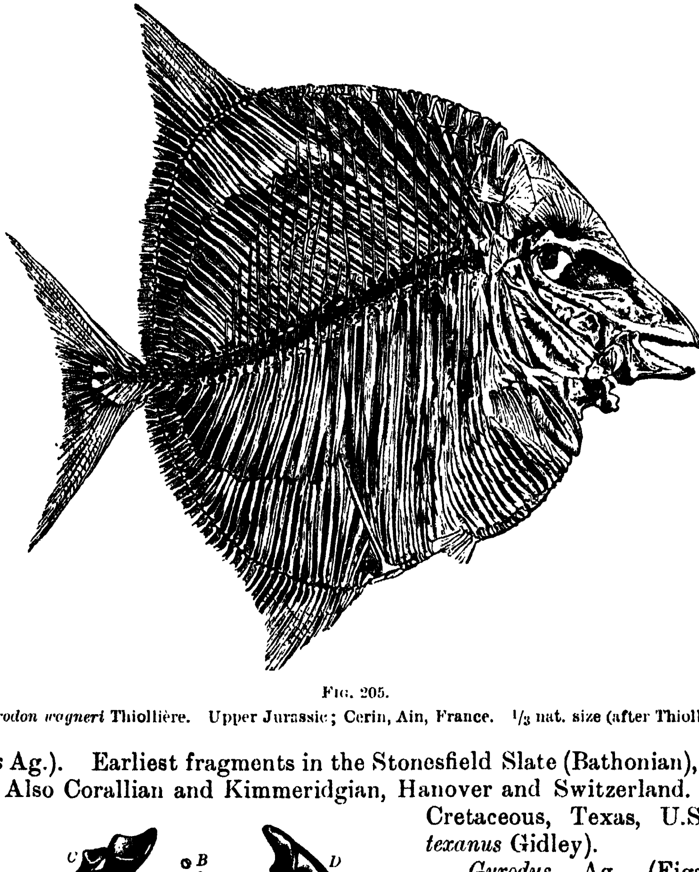


Fig. 205.
Microdon wagneri Thiollière. Upper Jurassic; Cerin, Ain, France. 1/3 nat. size (after Thiollière).

radiatus Ag.). Earliest fragments in the Stonesfield Slate (Bathonian), Oxfordshire. Also Corallian and Kimmeridgian, Hanover and Switzerland. Lower Cretaceous, Texas, U.S.A. (*M. texanus* Gidley).

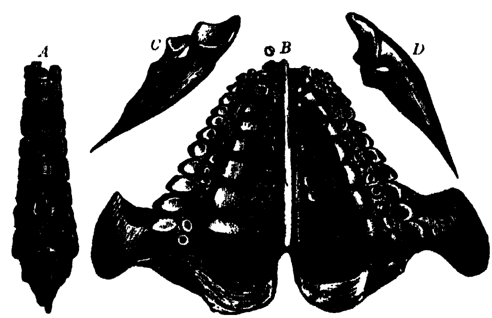


Fig. 206.
Microdon elegans Ag. Vomer (*A*), splenials of mandible (*B*), and anterior teeth of mandible, inner view (*C*), and outer view (*D*), nat. size. Upper Jurassic; Kelheim.

Gyrodus Ag. (Figs. 208-211).[1] Trunk completely covered with scales. Frontal profile steep. Vomer with five rows of rounded, bean-shaped teeth, of which the convex crown has a rugose border and mammillated apex; the middle row larger than the lateral rows. Splenial with four rows of similar teeth; dentary with four stout prehensile teeth. Caudal fin deeply forked, symmetrical. Common in the Upper Jurassic (Lithographic Stone) of Solenhofen, Eichstädt, Kelheim, Cerin (Ain); also in the

[1] *Weitzel, K.*, Abhandl. Senckenberg. Naturf. Ges., vol. xlii., p. 89, 1930.

Kimmeridgian of England, France, and Switzerland, in the Portlandian and Neocomian of France, Switzerland, and Isle of Wight, and the Tithonian of Sicily. *G. macrophthalmus cubensis* Gregory, from Upper Jurassic, Cuba. Some species from the Lithographic Stone (*G. titanius* Wagner) (Figs. 209-211) attain a length of 2 m. and depth of 1 m.

Mesturus Wagner.[1] Much resembling *Gyrodus*, but with more irregular teeth, rounded caudal fin, and scales often united above and below by jagged sutures. *M. verrucosus*

FIG. 207.

Microdon itieri Thiollière. Part of vertebral column. Upper Jurassic; Cerin. Nat. size (after Thiollière).

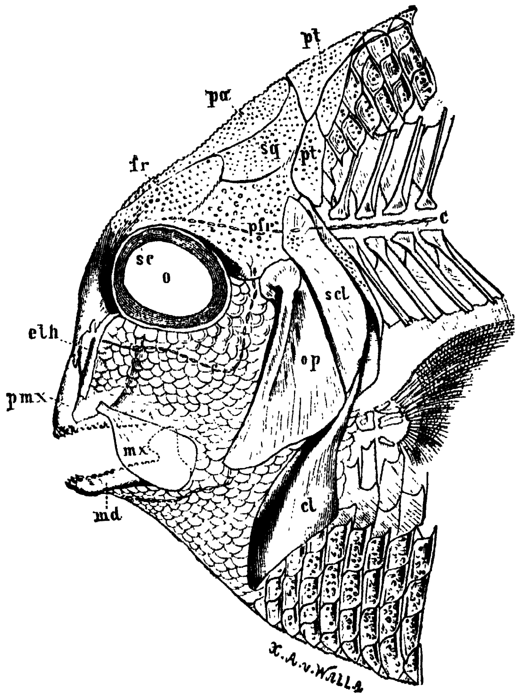


FIG. 208.

Head of *Gyrodus macrophthalmus* Ag. Upper Jurassic (Lithographic Stone); Kelheim, Bavaria. *c*, slime canals; *cl*, cleithrum; *eth*, ethmoid; *fr*, frontal; *md*, mandible; *mx*, maxilla; *O*, orbit; *op*, preoperculum; *pa*, parietal; *pfr*, postfrontal; *pmx*, premaxilla; *pt*, post-temporals; *sc*, sclerotic ring; *scl*, operculum; *sq*, squamosal.

Wagn., from Lithographic Stone of Bavaria. *M. leedsi* A. S. Woodw., represented by fine specimens displaying osteology from Oxford Clay, Peterborough.

Stemmatodus Heckel. Small, resembling *Microdon* but less deepened. Vomerine teeth in five, splenial in three rows, all teeth rounded and not very unequal in size. Lower Cretaceous; Castellamare.

Coelodus Heckel. Hinder half of trunk scaleless. Vomerine dentition with one median row of large, transversely elongated, smooth, oval teeth, and two lateral rows of small teeth. One row in the splenial dentition relatively very large, its teeth transversely elongated. Caudal fin either slightly excavated or convex mesially and slightly hollowed laterally. Upper Kimmeridgian (Lithographic Stone); Lérida, Spain. Portlandian; France. Purbeck and Wealden; England. Cretaceous of Istria, Dalmatia, and Southern

[1] *Woodward, A. S.*, Ann. Mag. Nat. Hist. [6], vol. xvii., p. 1, 1896.

Italy. Cenomanian and Turonian in Europe, Syria, Madagascar, and North America. Upper Senonian; Persia and Tunis.

Anomoeodus Forir (Fig. 212). Vomerine teeth in three or five longitudinal series, more or less irregular. Splenial dentition with one row relatively large, the lateral series more or less irregular, and not reaching the oral border of the bone. *A. subclavatus* Ag. sp., from Upper Cretaceous, Maastricht. *A. muensteri* Ag. sp. (Fig. 212), and other species from the European Greensand. Also North America.

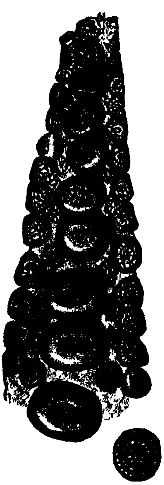
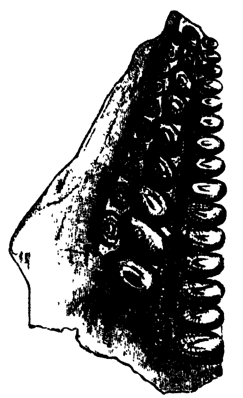


FIG. 209.
Gyrodus titanius Wagn. Vomerine plate with teeth, nat. size. Kelheim.



⅘ FIG. 210.
Gyrodus titanius Wagn. Right splenial with four rows of teeth, nat. size. Kelheim.

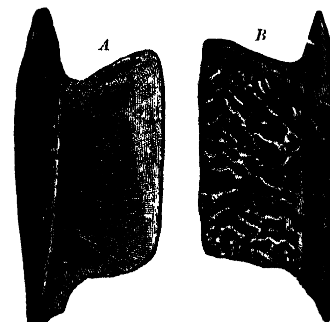


FIG. 211.
Gyrodus titanius Wagn. Scale, inner (*A*) and outer (*B*) aspects, nat. size. Kelheim.

Palaeobalistum Blv. Upper Cretaceous; Europe, Asia, and Brazil. Upper Eocene; Monte Bolca.

Coccodus Pictet. With median spine on skull and spines on pectoral arch.

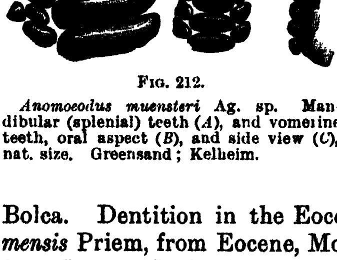


FIG. 212.
Anomoeodus muensteri Ag. sp. Mandibular (splenial) teeth (*A*), and vomerine teeth, oral aspect (*B*), and side view (*C*), nat. size. Greensand; Kelheim.

Xenopholis Davis. With rhombic overlapping scutes. Upper Cretaceous; Lebanon.

Acrotemnus Ag.[1] Grinding teeth compressed to an edge which is sometimes tuberculate. Upper Chalk; England and Belgium.

Polygyrodus White. *P. cretaceus* Ag. sp. English Chalk.

Pycnodus Ag. Trunk rather elongated, with slender caudal pedicle and forked caudal fin. Dorsal much more extended than the anal fin. Scales thin, absent on the caudal region. Teeth of the three middle rows of the vomer rounded, those of the two outer rows somewhat smaller and elliptical. *P. platessus* Blv. sp., from Upper Eocene, Monte Bolca. Dentition in the Eocene of several European localities. *P. mokattamensis* Priem, from Eocene, Mokattam Hills, Egypt. *P. lametae* A. S. Woodw., from Lameta Beds, Central Provinces, India.

[1] *Leriche, M.*, Bull. Soc. Belge Géol., vol. xxv., Proc.-Verb., p. 162, 1911.

Family 5. **Eugnathidae.**

Trunk slender. Mandibular suspensorium inclined backwards and gape of mouth large. Marginal teeth conical. Cranial and facial bones moderately robust,

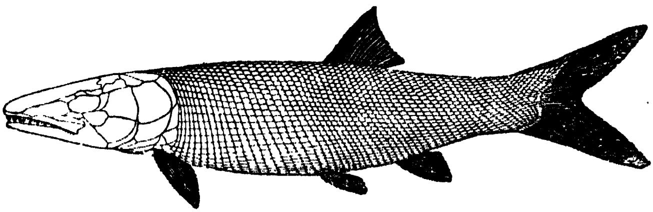


FIG. 213.
Eugnathus orthostomus Ag. Restoration by A. S. Woodward, about $^1/_7$ nat. size. Lower Lias; Lyme Regis.

externally enamelled, and opercular apparatus complete. Snout not produced. Vertebral column rarely more than incomplete rings. Fin rays stout, fulcra con-

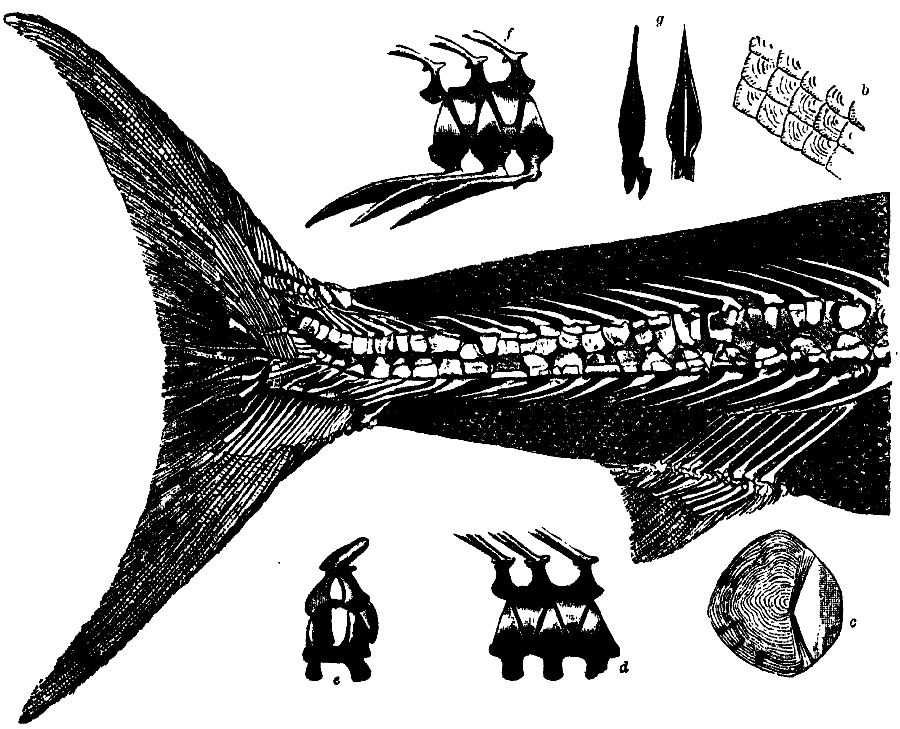


FIG. 214.
a, *Caturus maximus* Ag., tail. *b-g*, *Caturus furcatus* Ag. Upper Jurassic (Lithographic Stone); Bavaria. *b*, *c*, scales, nat. size and enlarged; *d*, *e*, abdominal vertebrae in side view and front view; *f*, caudal vertebrae; *g*, haemal spines in front view.

spicuous. Dorsal fin short and acuminate. Scales rhombic, sometimes thin and with rounded angles. Triassic to Cretaceous.

Allolepidotus Deecke (*Plesiolepidotus* Schlosser). Middle and Upper Triassic; Europe.

Eugnathus Ag. (*Heterolepidotus* Egerton; *Brachyichthys* Winkler; *Isopholis* Zittel) (Fig. 213). Large, conical, pointed laniary teeth and numerous smaller pointed teeth between these. Head and opercular bones smooth or tuberculated. Fins powerful, the dorsal arising opposite the pelvic pair, stouter and longer than the anal fin; caudal fin forked. Scales rather thick, mostly broader than deep, and with serrated hinder border. The type species, *E. orthostomus* Ag. (Fig. 213), a slender fish, common in the Lower Lias of Lyme Regis, Dorset. Other species in the Lias, and ranging upwards to the Lithographic Stone of Europe (*E. microlepidotus* Ag.). *Heterolepidotus merzbacheri* Leriche, from Mesozoic of Tian-Schan (Abh. k. bay. Akad. Wiss., math.-phys. Cl., vol. xxvii., p. 306, 1916).

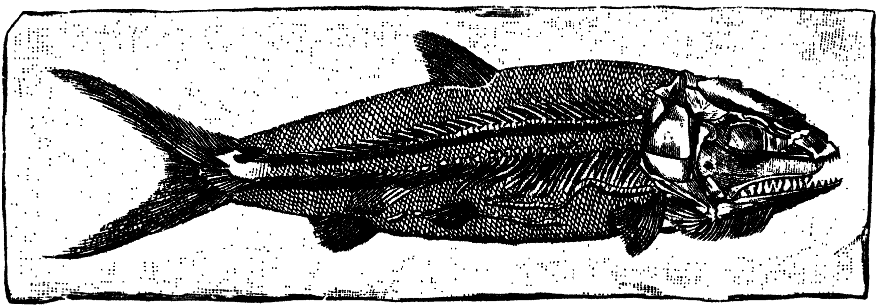


FIG. 215.
Caturus elongatus Ag. Upper Jurassic (Lithographic Stone); Cerin, Ain, France. 1/2 nat. size.

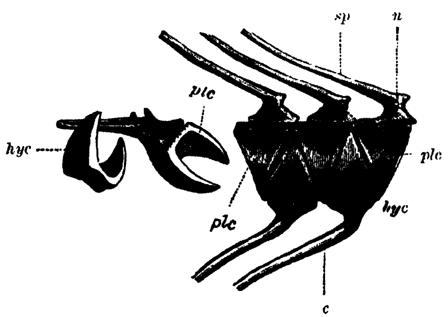


FIG. 216.
Callopterus agassizi Thiollière. Vertebrae, about nat. size. *c*, caudal haemal spine; *hyc*, hypocentrum; *n*, neural arch; *plc*, pleurocentrum; *sp*, neural spine. Upper Jurassic (Lithographic Stone); Bavaria.

Caturus Ag. (*Conodus*, *Uraeus* Ag.) (Figs. 214, 215). Essentially identical with *Eugnathus*, but scales thinner, more deeply overlapping, and less narrowed near the ventral border of the fish. Endoskeleton of trunk usually well displayed in the fossils, showing hemi-vertebrae, short ribs, and free neural spines in the abdominal region. Ranging from the Trias to the Upper Jurassic, especially fine specimens being known from the Lower Lias of England (*C. heterurus* Ag. sp., etc.), the Upper Lias of Würtemberg (*C. smithwoodwardi* White), and the Lithographic Stone of France, Bavaria, Würtemberg, and Lérida, Spain (*C. furcatus*, *elongatus*, *maximus* Ag., etc.). *C. deani* W. K. Gregory. Jurassic; Cuba.

Strobilodus Wagner; *Thlattodus*, *Ditaxiodus* Owen. Large fishes resembling *Caturus*. Upper Jurassic of Europe.

Callopterus Thiollière (Fig. 216). As *Caturus*, but dorsal fin opposed to anal fin. Lithographic Stone of Bavaria and France. *C. insignis* Traq. Wealden; Belgium.

Eurycormus Wagner (Fig. 217). Much resembling *Caturus*, but vertebral column consisting of hemi-vertebrae which become two similar complete rings in the caudal region. Dentition comparatively feeble. *E. speciosus* Wagn., from Lithographic Stone, Bavaria and Würtemberg. Other species in Oxford and Kimmeridge Clays, England.

Osteorachis Egerton (*Isocolum*, *Harpactes*, *Harpactira* Egerton). Marginal teeth relatively large, inner teeth slender and clustered. Large hemi-vertebrae, not fusing into rings. Scales thin. *O. macrocephalus* Eg. Lower Lias; Dorset. *O. leedsi* A. S. Woodw. Oxford Clay; Peterborough.

Ptycholepis Ag.[1] Head and opercular bones ornamented with ridges of ganoine; teeth minute. Scales thick, much broader than deep, externally marked with longitudinal grooves. *P. bollensis* Ag., from Upper Lias of England, France, Bavaria, and Würtemberg. Other species in Lower Lias of England. Smaller species in Trias of Raibl (Carinthia), Besano (Lombardy), and Connecticut, U.S.A.

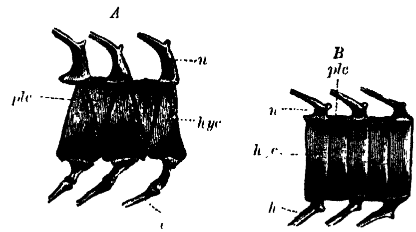


Fig. 217.

Eurycormus speciosus Wagner. Abdominal (*A*) and caudal (*B*) vertebrae. *c*, rib; *h*, haemal arch; other letters as in Fig. 216. Upper Jurassic (Lithographic Stone); Bavaria.

Neorhombolepis A. S. Woodward. Vertebral centra either ring-shaped or completely ossified. Scales thick, the majority broader than deep. *N. excelsus* A. S. W., English Lower Chalk. Also in Wealden, England, and Lower Cretaceous, Bahia, Brazil.

Lophiostomus Egerton. External bones strongly enamelled and a pair of bony prominences on cranial roof behind the eyes. Ring vertebrae. English Chalk and Cambridge Greensand.

Otomitla Felix. Neocomian; Mexico.

Family 6. Amiidae.

(*Megaluridae* Zittel; *Halecomorphi* Cope.)

Marginal teeth conical, powerful. Branchiostegal rays broad and few; jugular plate large. Vertebral column usually well ossified. Of vertebrae, if present, the pleurocentra and hypocentra forming complete alternating discs in part of the caudal region, the alternate discs bearing the neural and haemal arches. Fulcra almost or completely absent. Scales thin and cycloid, deeply overlapping. Upper Jurassic to Recent.

Liodesmus Wagner (*Lophiurus* Vetter). Notochord persistent, without any beginning of centra. Fulcra absent. Dorsal fin short-based and median; caudal fin fan-shaped or slightly forked. Scales very small. *L. gracilis* Ag. sp. and *L. sprattiformis* Wagn., from Lithographic Stone of Bavaria.

Megalurus Ag. (*Urocles* Jordan) (Figs. 218, 219). Vertebral column much produced into the upper caudal lobe; centra smooth; caudal hemi-vertebrae rather elongated. Fulcra present. Dorsal fin considerably extended, arising opposite the pelvic fins, and reaching the hinder end of the anal fin; caudal fin convex behind, very large. Several species in the Upper Jurassic (Litho-

[1] *Hennig, E.*, *Ptycholepis bollensis*, Jahresh. Ver. Vaterl. Naturk. Württ., 1918, p. 173.—*Woodward, A. S.*, Proc. Yorks. Geol. Polyt. Soc., vol. xiii., p. 36, 1895.

graphic Stone) of Bavaria, Würtemberg, Ain (France), and Lérida (Spain). *M. mawsoni* A. S. Woodw., from Lower Cretaceous, Bahia, Brazil.

Amiopsis Kner. As *Megalurus*, but sides of vertebral centra pitted. *A. prisca* Kner, from Lower Cretaceous, Istria. *A. damoni* Egert. sp., from English Purbeck Beds. *A. dolloi* Traq., from Wealden, Belgium.

Opsigonus Kramberger. Lower Cretaceous; Dalmatia.

Amia Linn.[1] (*Cyclurus, Notaeus* Ag.) (Figs. 168 *B*, 220). Fulcra absent. Dorsal fin arising in front of the pelvic pair and extending to the caudal fin. Living in North America; fossil in Lower Eocene to Lower Miocene fresh-

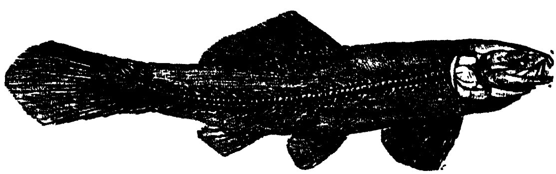


FIG. 218.
Megalurus elegantissimus Wagn. Upper Jurassic; Solenhofen, Bavaria. 2/3 nat. size.

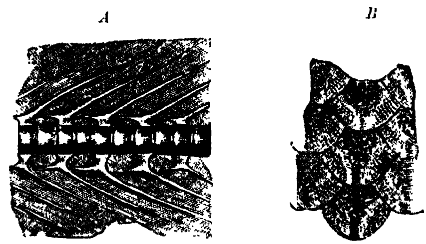


FIG. 219.
Megalurus polyspondylus Münst. Upper Jurassic; Kelheim. *A*, caudal portion of vertebral column, nat. size. *B*, scales, enlarged.

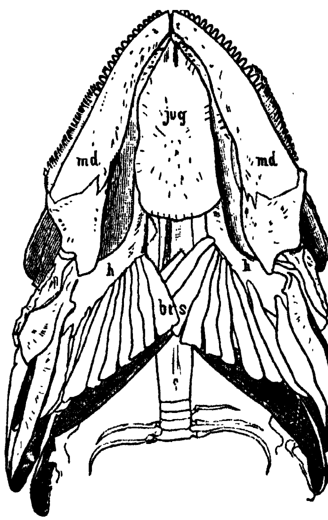


FIG. 220.
Amia calva Linn. Head, from beneath. Recent; South Carolina. *brs*, branchiostegal rays; *h*, ceratohyal; *jug*, jugular plate; *md*, mandible.

water formations of Europe and North America. *A.* (*Notaeus*) *longicauda* Ag. (Montmartre), *A.* (*Cyclurus*) *valenciennesi* Ag. (Armissan), *A. kehreri* Andreae (Messel, near Darmstadt), *A. anglica* Newton (Isle of Wight), *A.* (*Cyclurus*) *macrocephala* Reuss (Bohemia).

Pappichthys Cope; *Protamia, Hypamia* Leidy. Eocene; Wyoming, U.S.A. Upper Cretaceous; Alberta, Canada. *Protamia* also from Eocene of Russia.

Stylomyleodon Russell.[2] Resembling *Amia*, but with inner teeth blunt for crushing. Upper Cretaceous and Lower Eocene; Alberta, Canada. Lower Eocene; Wyoming, U.S.A. ?*Kindleia* Jordan. Upper Cretaceous; Alberta.

Paramiatus Romer and Fryxell.[3] A deep-bodied Amioid from the Eocene Green River Shales of Wyoming, U.S.A.

[1] *Andreae, A.*, Abh. Senckenb. Naturf. Ges., vol. xviii., p. 359, 1894.—*Leriche, M.*, Bull. Soc. Belge Géol., vol. xxii., p. 121, 1908.—*Newton, E. T.*, Quart. Journ. Geol. Soc., vol. lv., p. 1, 1899.

[2] *Jordan, D. S.*, Canadian Field Naturalist, vol. xli., p. 145, 1927; *Russell, L. S.*, Amer. Journ. Sci., vol. xv., pp. 103, 264, 1928; vol. xvii., p. 369, 1929.

[3] *Romer, A. S.*, and *Fryxell, F. M.*, *Paramiatus gurleyi*. Amer. Journ. Sci., vol. xvi., p. 519, 1928.

Family 7. **Pachycormidae.**[1]

(*Microlepidoti* and *Cyclolepidoti* Zittel.)

Trunk elongate or fusiform, and the mesethmoid forming a prominent rostrum, separating the premaxillae in the median line. Gape of mouth large, and marginal teeth conical. Opercular apparatus complete, with very numerous branchiostegal rays. Vertebral arches very numerous and closely arranged, with or without hemi-vertebrae; the last haemal expanded to support the lower lobe of the powerful caudal fin. Fin rays slender and closely set; fulcra minute or absent. Scales thin and rhombic, sometimes with rounded angles. Upper Lias to Upper Cretaceous.

Pachycormus Ag. (*Cephenoplosus* Sauvage) (Fig. 221). Large, salmon-shaped fishes, with hemi-vertebrae only in the caudal region. Cranial roof raised

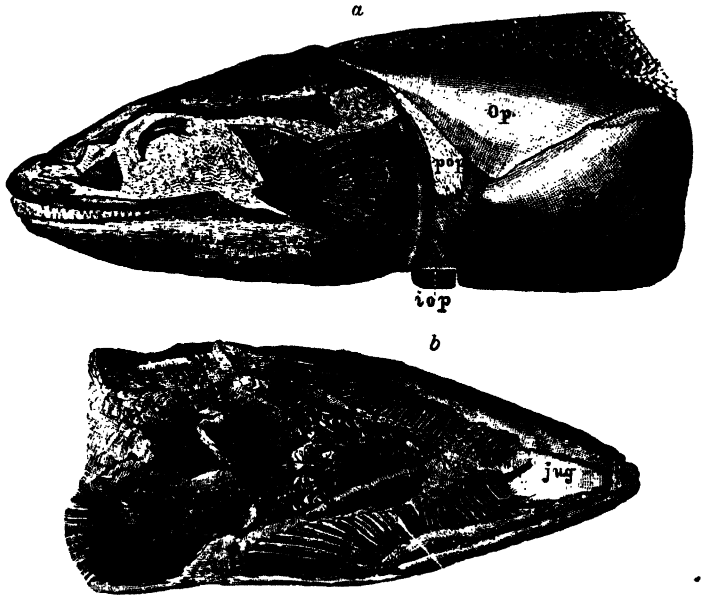


FIG. 221.

Pachycormus macropterus Blainville sp. Head from the side (*a*) and from beneath (*b*), reduced. Upper Lias; Ilminster, England. *iop*, interoperculum; *jug*, jugular plate; *md*, mandible; *mx*, maxilla; *op*, operculum; *pop*, preoperculum; *so*, suborbitals; *sop*, suboperculum. $^1/_2$ nat. size.

into a median ridge behind. Operculum, suboperculum, and suborbitals very large. Rays of all the fins with distant articulations. Pectoral fins large; pelvic fins absent; short dorsal fin arising in front of the anal; deeply forked caudal with elongated fulcra on each lobe. *P. macropterus* Blv. sp. (Fig. 221), and other species in the Upper Lias of Germany, France, Belgium, and England.

Saurostomus Ag. As *Pachycormus*, but head relatively low and broad, the occipital region not raised into a ridge. Anterior pectoral fin ray produced apparently into a tactile organ. *S. esocinus* Ag. Upper Lias; Würtemberg and England.

Euthynotus Wagner (*Heterothrissops, Pseudothrissops* Sauvage) (Fig. 222).

[1] *Woodward, A. S.*, *Pachycormus* and *Hypsocormus* from the Jurassic of Normandy. Mém. Soc. Linn. Normandie, vol. xxiii, p. 29, 1908.—*Saurostomus*. Geol. Mag., 1916, p. 49.

Hemi-vertebrae present. Fin fulcra minute. Pelvic fins present; dorsal fin opposed to much-extended anal fin. Scales rhombic, rounded at the angles. *E. speciosus* Wagn., and other species in the Upper Lias of Germany, France, and England.

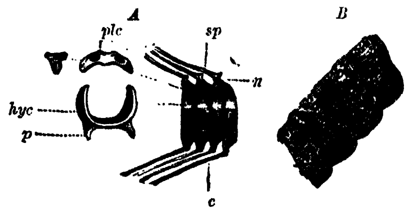


FIG. 222.

Euthynotus micropodius Ag. sp. Upper Lias; Boll, Wurtemberg. *A*, vertebrae (*c*, haemal arches; *hyc*, hypocentrum; *n*, neural arches; *p*, parapophyses; *plc*, pleurocentrum; *sp*, neural spine). *B*, scales. Nat. size.

Sauropsis Ag. (*Diplolepis* Vetter). Elongate fusiform. No hemi-vertebrae. No fulcra. Pelvic fins present; dorsal fin opposed to much-extended anal fin. *S. latus* Ag., *S. veruinalis* White. Upper Lias; Würtemberg. *S. longimanus* Ag. Lithographic Stone; Bavaria. *S.* (?) *woodwardi* Gregory. Jurassic; Cuba.

Prosauropsis Sauvage. Differing from *Sauropsis* in short anal fin. *P. elongatus* Sauv. Upper Lias; Yonne, France.

Eugnathides W. K. Gregory. Jurassic; Cuba.

Hypsocormus Wagner (Fig. 223). Large fishes, with very small rhombic scales, much resembling *Pachycormus*, but with larger round teeth, small pelvic fins, and a much extended anal fin. Large teeth rounded in section, of complex structure, not in sockets. *H. insignis* Wagn., from Lithographic Stone of Bavaria. *H. leedsi* A. S. Woodw., from Oxford Clay, Peterborough.

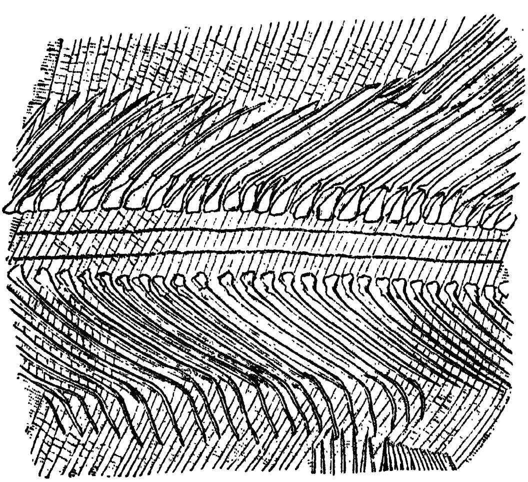


FIG. 223.

Hypsocormus insignis Wagn. Portion of trunk. 1/3 nat. size. Upper Jurassic (Lithographic Stone); Eichstädt, Bavaria.

FIG. 224.

Tooth of *Protosphyraena ferox* Leidy. Upper Chalk; Maastricht. Nat. size.

Orthocormus Weitzel.[1] Lithographic Stone; Bavaria.

Asthenocormus A. S. Woodw. (*Agassizia* Vetter *nec* Valenciennes). Trunk elongate and head relatively large. Teeth minute and clustered. No hemi-vertebrae. Pectoral fins very large and sickle-shaped; pelvic fins absent; dorsal in advance of anal fin. *A. titanius* Wagn. sp., about 2 m. long, from Lithographic Stone, Bavaria.

[1] *Weitzel, K.*, Natur und Museum (Frankfurt), vol. 60, p. 26, 1930; also Abhandl. Senckenberg. Naturf. Ges., vol. xlii., p. 101, 1930.

Leedsia A. S. Woodw. A gigantic fish known by fragments from the Oxford Clay of Peterborough (*L. problematica* A. S. W.) and Normandy, and the Kimmeridge Clay of Dorset.

Protosphyraena Leidy[1] (*Erisichthe*, *Pelecopterus* Cope) (Figs. 224-227). Known only by the head and fins much resembling those of *Hypsocormus*, but teeth laterally compressed, in sockets, and snout more produced. *P. ferox* Leidy, and other species, in the Upper Cretaceous of Europe and North America. Teeth from Egypt and Patagonia. The teeth were wrongly ascribed to *Saurocephalus* Harlan, by Agassiz, the pectoral fins to *Ptychodus* Ag.

FIG. 225.
Protosphyraena nitida Cope. Rostrum from beneath, showing pair of vomerine teeth, $^1/_4$ nat. size. Upper Chalk ; Kansas.

FIG. 226.
Protosphyraena sp. Articulation of pectoral fin with pectoral arch. Upper Chalk ; Kansas. *bas*, basals ; *co*, coracoid ; *pct*, fin rays ; *sc*, scapula. $^1/_3$ nat. size (after Hay).

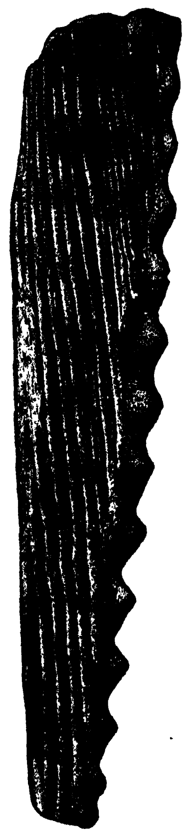


FIG. 227.
Protosphyraena sp. Part of pectoral fin. English Chalk. $^1/_2$ nat. size (after A. S. Woodward).

Family 8. **Aspidorhynchidae.**[2]

Very slender, elongated fishes, with snout elongated and pointed. Maxilla loose ; mandible with a movable predentary or presymphysial bone. Teeth conical, pointed. Branchiostegal rays numerous. Notochord with ring-vertebrae. Caudal fin externally homocercal. Fin fulcra minute. Scales rhombic, some deepened on flank. Bathonian to Upper Cretaceous.

Aspidorhynchus Ag. (Fig. 228). Thin, slender fishes, attaining a metre in length, with enamelled scales, which are more or less rugose and not remarkably thick. Foremost scales of lateral line not deeper than those immediately beneath. Pectoral fin with very broad rays, which are jointed only in their distal quarter; no fulcra. Pelvic fins somewhat behind the middle point of the trunk. Anal fin opposed to the small dorsal fin, each with minute fulcra. Caudal fin

[1] *Felix, J.*, Zeitschr. Deutsch. Geol. Ges., vol. xlii., p. 278, 1890.—*Loomis, F. B.*, Palaeontogr., vol. xlvi., p. 215, 1900.—*Woodward, A. S.*, Ann. Mag. Nat. Hist. ser. 6, vol. xiii., p. 510, 1894.

[2] *Assmann, P.*, Über *Aspidorhynchus*. Archiv f. Biontologie, vol. i., p. 49, 1906.—*Reis, O.*, Über *Aspidorhynchus*, *Belonostomus*, und *Lepidosteus*. Sitzungsb. k. bay. Akad. Wiss., math.-phys. Cl., 1887, p. 151.

deeply forked, with delicate fulcra. Lower jaw much shorter than the snout, which is formed by the mesethmoid and premaxillae. The oldest known species is *A. crassus* A. S. Woodw., from the Stonesfield Slate (Bathonian) of Oxfordshire. *A. euodus* Egerton, from Oxford Clay. Well preserved fishes

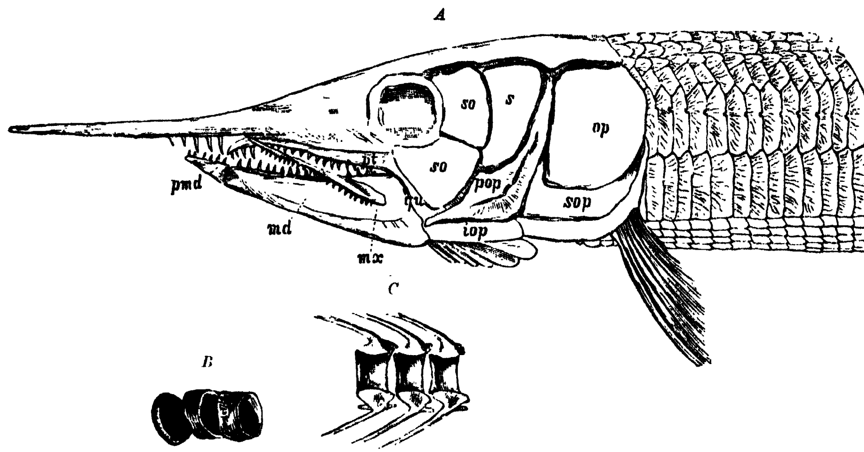


FIG. 228.

Aspidorhynchus acutirostris Blv. sp. Upper Jurassic (Lithographic Stone); Solenhofen. *A*, head and part of trunk; *iop*, interoperculum; *md*, mandible; *mx*, maxilla; *op*, operculum; *pmd*, predentary; *pop*, preoperculum; *pt*, pterygoid; *qu*, quadrate; *s*, *so*, suborbitals (the division between *s* and *so* is a crack); *sop*, suboperculum. *B*, vertebral rings. *C*, three vertebrae of caudal region. Nat. size.

in the Lithographic Stone of Bavaria (*A. acutirostris* Blv. sp.) and France; also in the English Purbeck Beds (*A. fisheri* Egerton).

Belonostomus Ag. (*Vinctifer* Jordan). As above, but mandible almost as long as the snout, and all scales of lateral line deeper than those immediately beneath. Kimmeridgian to Upper Cretaceous. Fine skeletons in the Lithographic Stone of Bavaria (*B. sphyraenoides* Ag., etc.) and France, and the Cretaceous of Europe. Jaws and scales of *B. cinctus* Ag. in the Chalk of England and N. France. Other species in the Cretaceous of Mexico (*B. ornatus* Felix), Brazil (*B.* [*Vinctifer*] *comptoni* Ag. sp.), and Queensland (*B. sweeti* Eth. and Woodw.).

Family 9. **Lepidosteidae.** Bony pikes.[1]

Trunk elongated, with thick, enamelled rhombic scales. Snout much produced, the very long maxilla divided by a series of vertical sutures into several pieces, which bear large pointed laniary teeth and small clustered teeth; premaxilla short and toothed. Vertebral column completely ossified; vertebrae opisthocoelous. All fins with biserial fulcra. Dorsal and anal finsremote, near the rounded caudal fin. Upper Cretaceous to Recent.

Lepidosteus Lacépède (Fig. 229), the only genus of this family, survives in the rivers of the southern United States, Central America, and Cuba. Complete individuals occur in the Eocene and Lower Miocene of Europe and North America. *L. atrox* Leidy, from the Middle Eocene Green River

[1] *Eastman, C. R.*, Fossil Lepidosteids from the Green River Shales of Wyoming. Bull. Mus. Comp. Zool. Harvard, vol. xxxvi., p. 67, 1900. Also Geol. Mag. [4], vol. vii., p. 54, 1900.

Shales of Wyoming, attains a length of 1·7 m. *L. fimbriatus* Wood, from Oligocene, Hordwell, Hampshire. *L. indicus* A. S. Woodw., from the Lameta Beds, Central Provinces, India. *L.*

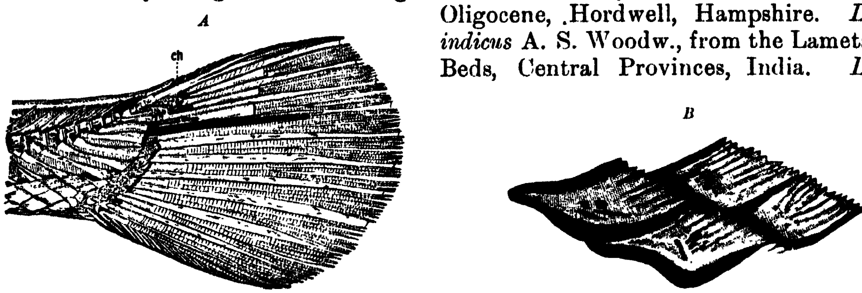


FIG. 229.
Lepidosteus osseus Linn. Tail (*A*) and scales (*B*). *ch*, upturned end of vertebral column. Recent; North America.

(*Clastes*) *lusitanicus* Sauvage, from Garumnian, Portugal. Stensiö has observed rudiments of the clavicles in the existing species.

Clastes Cope. Eocene; Wyoming and Utah, U.S.A.

Order 4. HALECOSTOMI.

Vertebral centra complete, but usually pierced by persistent strand of notochord. Head well ossified. Premaxilla relatively small; both this and maxilla loose. Mandibular ramus of not more than two or three elements. Branchiostegal rays, sometimes with median jugular plate. No clavicle. Supports of dorsal and anal fins equal in number to the dermal rays. Caudal fin hemi-heterocercal.

Family 1. **Pholidophoridae.**[1]

Trunk fusiform. Gape of mouth wide; two supramaxillary plates; teeth small and conical. Fulcra present; dorsal and anal fins small. Scales rhombic, but thin and deeply overlapping; no intermuscular bones. Triassic to Upper Jurassic.

Prohalecites Deecke. Trias; Raibl, Carinthia, and Perledo, Lombardy.

Pholidophorus Ag. (Figs. 230-232). In shape and size like herrings. Scales deeper than wide on the flank, smooth or finely striated and serrated. Small dorsal fin opposed to the pelvic pair. Caudal fin externally homocercal, deeply forked; a large, unpaired dorsal scale often at its base. Common in the Alpine Trias of Raibl (*P. bronni* Kner) and Seefeld (*P. pusillus* Ag.); in the Lower Lias of Lyme Regis (*P. bechei* Ag., *P. limbatus* Ag.), Upper Lias of Whitby, Calvados, Würtemberg, and Bavaria (*P. germanicus* Quenst.); in the Lithographic Stone of Bavaria and France; in the Purbeck Beds of England, Wealden of Belgium, and Lower Jurassic of the Black Hills, South Dakota, and near Santa Rosa, New Mexico. Also Jurassic, China; Hawkesbury Formation, New South Wales; Karroo Formation, South Africa and Congo.

Baleiichthys Rohon. As *Pholidophorus*, but dorsal fin more remote. Jurassic; Irkutsk, Siberia.

Thoracopterus Bronn (*Pterygopterus* Kner). Pectoral fins much enlarged, and dorsal opposed to anal fin. Trias; Raibl, Carinthia; and Lunz, Austria.

[1] *Biese, W.*, Pholidophoriden aus den lithographischen Schiefern Bayerns. Neues Jahrb. f. Min., etc., Beil.-Bd. lviii., p. 50, 1927.

Gigantopterus Abel. Upper Trias ; Lunz, Austria.

Ceramurus Egerton. Scales almost or completely absent on flanks ; a short series of stout ganoid ridge-scales on hinder half of caudal region above and below. *C. macrocephalus* Eg. Purbeck Beds ; Wiltshire and Dorset.

Pleuropholis Egerton (Fig. 233). Scales thick, those of middle of flank much deepened, dorsal and ventral scales small and rhomboidal. Lateral line deflected, traversing upper row of ventral scales. Dorsal and anal fins extended and opposed. *P. attenuata* Eg., and other species from English Purbeck Beds. *P. egertoni* Wagner and other species from Lithographic Stone of Germany and France. Wealden ; Belgium and Lebanon (*P. koerti* Janensch).

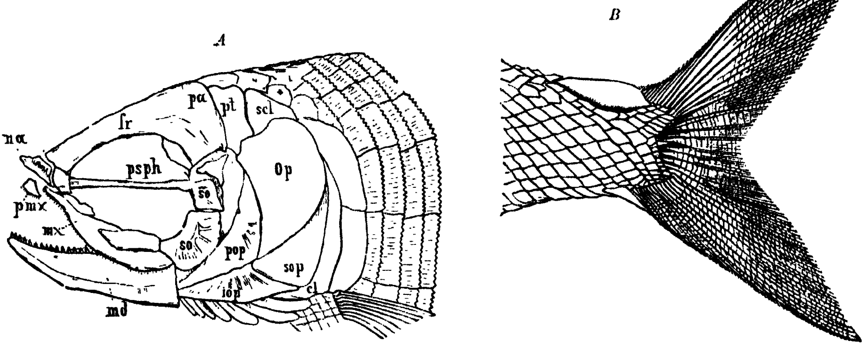


FIG. 230.

Pholidophorus striolaris Ag. Head (*A*) and tail (*B*), nat. size. Upper Jurassic (Lithographic Stone); Eichstädt. *cl*, cleithrum ; *fr*, frontal ; *iop*, interoperculum ; *md*, mandible ; *mx*, maxilla ; *na*, nasal ; *op*, operculum ; *pa*, parietal ; *pmx*, premaxilla ; *pop*, preoperculum ; *psph*, parasphenoid ; *pt*, post-temporal ; *scl*, supracleithrum ; *so*, suborbitals ; *sop*, suboperculum.

FIG. 231.

Pholidophorus micronyx Ag. Inner view of scales. Upper Jurassic (Lithographic Stone) ; Eichstädt. Nat. size.

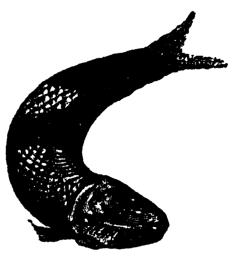


FIG. 232.

Pholidophorus pusillus Ag. Upper Trias ; Seefeld, Tyrol. Nat. size.

? *Archaeomene* A. S. Woodw. Apparently without ring-vertebrae. Dorsal and anal fins opposed. Scales thin and almost cycloidal ; none deepened. *A. tenuis* A. S. W., 12 cm. long. Upper Hawkesbury-Wianamatta Beds ; Talbragar, New South Wales.

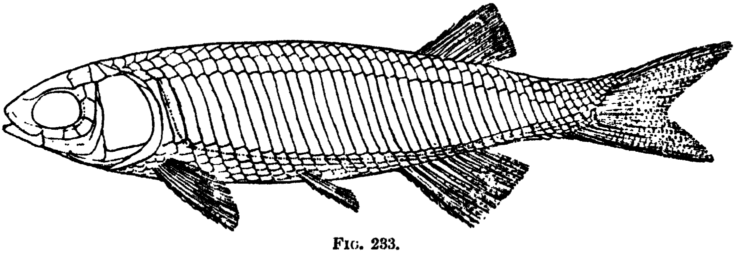


FIG. 233.

Pleuropholis formosa A. S. Woodw. Restoration by A. S. Woodward, slightly enlarged. Purbeck Beds ; Wiltshire.

Family 2. **Oligopleuridae.**

As Pholidophoridae *but scales very thin and cycloid, deeply overlapping.* Upper Jurassic to Upper Cretaceous.

Oligopleurus Thiollière (Fig. 234). Teeth very small, and mandible prominent. Vertebral centra not pitted. Dorsal fin short-based, opposed to

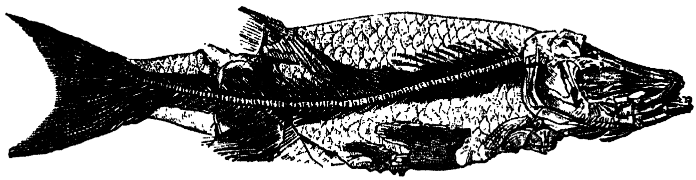


FIG. 234.
Oligopleurus esocinus Thioll. Upper Jurassic (Lithographic Stone); Cerin, Ain, France. 1/4 nat. size (after Thiollière).

anal fin. Caudal fin slightly forked. Scales rather large. *O. esocinus* Thioll., from Lithographic Stone, Cerin (Ain, France).

Oeonoscopus Costa (*Attakeopsis* Thioll.; *Macrorhipis* Wagn.). Almost as above, but vertebral centra with two lateral pits and greater portion of dorsal in advance of anal fin. *O. petraroiae* Costa, from Lower Cretaceous, Pietraroja, Prov. Benevento, Italy. Other species in French and German Lithographic Stone.

Spathiurus Davis (*Amphilaphurus* Davis). With much extended dorsal fin. *S. dorsalis* Davis. Upper Cretaceous; Mount Lebanon.

Family 3. **Leptolepidae.**

Trunk elegantly fusiform. Head with delicate membrane bones and well-developed cheek plates, more or less enamelled; parietals meeting in middle line, flanked by large squamosals. Gape of mouth wide; two supramaxillary plates; teeth small and conical. Intermuscular bones present. Fulcra absent; dorsal and anal fins small. Scales thin and cycloidal, ganoid and with bony layer. Upper Lias to Lower Cretaceous.

Lycoptera Müller.[1] Teeth minute. Dentary bone with no thickening. Pectoral fins much larger than pelvic pair; dorsal opposite anal fin; caudal

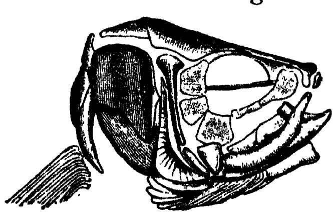


FIG. 235.
Head of *Leptolepis knorri* Ag. Upper Jurassic; Kelheim. Reduced.

FIG. 236.
Leptolepis sprattiformis Ag. Upper Jurassic; Eichstädt. Nat. size.

fin forked. *L. middendorffi* Müller. Jurassic; Turgá, Siberia. Other species scarcely more than 10 cm. in length from Jurassic of China.

Leptolepis Ag. (*Tharsis* Giebel; *Sarginites*, *Megastoma* Costa; *Liassolepis*

[1] *Cockerell, T. D. A.*, Bull. Amer. Mus. Nat. Hist., vol. li., art. viii., 1925.—*Reis, O. M.*, Rech. géol. et min. Chemin de Fer de Sibérie, livr. 29, p. 5. St. Petersburg, 1909.

Jaekel) (Figs. 235, 236). Usually small fishes. Dorsal fin in front of anal fin, which is not much extended. Dentary bone sharply rising into a thickened obtuse elevation near its anterior end. Teeth minute. *L. bronni* Ag., and other comparatively small species in the Upper Lias of England, France, and Germany. *L. dubius* Blv. sp., *L. sprattiformis* Ag. (Fig. 236), and other species in the Upper Jurassic (Lithographic Stone) of Bavaria, France, and Lérida, Spain; also from the English Purbeck Beds, the Wealden of Belgium and England, the Lower Cretaceous of Naples, the Isle of Lesina, Dalmatia, and the Hawkesbury-Wianamatta Formation of New South Wales. Fragments from King Charles Land, Spitzbergen, Persia, and Cuba.

Tharrhias Jordan and Branner (*Cearana* J. and B.).[1] Cretaceous; Ceará, Brazil.

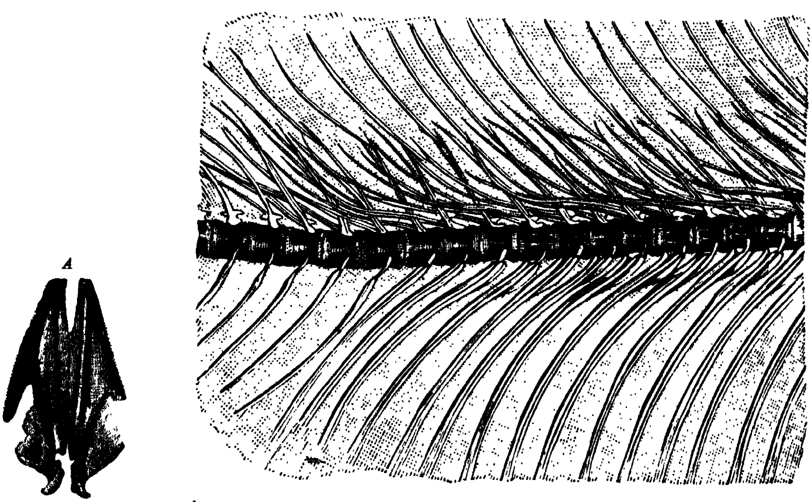


FIG. 237.

Thrissops formosus Ag. Two rami of lower jaw (*A*) and middle part of vertebral column (*B*). Upper Jurassic (Lithographic Stone); Kelheim. Nat. size.

Aethalion Münster. Nearly resembling *Leptolepis*, but dentary bone of mandible gradually deepening from the symphysis backwards without any marked thickening. Lithographic Stone; Bavaria and Lérida, Spain. Wealden; Belgium and England (*A. valdensis* A. S. W., about 40 cm. long). L. Cretaceous; Castellamare, Naples.

Thrissops Ag. (Fig. 237). The short dorsal fin opposed to the much-extended anal fin. Ribs very stout. Upper Jurassic and Lower Cretaceous of Europe, the type species being *T. formosus* Ag. (Fig. 237), from the Bavarian Lithographic Stone, 50 cm. long. One specimen[2] shows six or seven small skeletons of unborn young above the intestine, which is marked by a spiral valve. *T. molossus* A. S. W., English Purbeck Beds. Wealden; Belgium and England. *T. volgensis* Kozlov. Lower Volgian; Simbirsk, Russia.

Pachythrissops A. S. Woodw. (*Parathrissops* Eastman *nec* Sauvage). Head as in *Leptolepis*, but the elevation of the dentary relatively broad and less

[1] *Jordan, D. S.*, Mon. Serv. Geol. e Mineral. Brasil, vol. iii., p. 20, 1923.

[2] *Neumayer, L.*, Ein vivip rer Fisch aus dem lithographischen Schiefer von Kelheim. Centralbl. f. Min., etc., 1929, p. 499.

thickened. Vertebral centra stout. Dorsal and anal fins acuminate, not much extended, opposed. Scales very delicate. *P. laevis* A. S. W. Purbeck Beds; Dorset. *P. vectensis* A. S. W., at least a metre in length. Wealden; Isle of Wight and Sussex.

Eurystethus Sauvage. Upper Jurassic (Lithographic Stone); Ain, France.
Vidalia Sauvage. Upper Jurassic (Lithographic Stone); Lérida, Spain.

Haplospondylus Cabrera. Lower Cretaceous; Lake San Martin, Santa Cruz, Argentina.

Sub-Class 7. TELEOSTEI.[1] Bony fishes.

Skin with thin, elastic, cycloid or ctenoid scales, rarely with bony plates. Skull ossified, and jaws hyostylic. A parasphenoid bone. Mandible simple, each ramus consisting of only two or three elements. Vertebral column ossified. Intermuscular bones more or less numerous. Fin fulcra absent. Supports of dorsal and anal fins equal in number to the dermal rays; caudal fin often both internally and externally homocercal. In the living forms—optic nerves completely decussating, bulbus arteriosus of the heart with only two valves, and intestine without a spiral valve.

The distinction between the bony fishes and ganoids consists partly in the dermal skeleton and partly in anatomical characters, which cannot usually be verified by palaeontologists. The two Sub-Classes are most closely related to each other, and the line of demarcation between the *Protospondyli* or *Halecostomi* and the *Isospondyli* is sometimes almost obliterated. Among *Teleostei* the

[1] *Arambourg, C.*, Révision des poissons fossiles de Licata (Sicile). Ann. Paléontologie, vol. xiv., p. 39, 1925.—Les Poissons fossiles d'Oran. Matér. Carte géol. Algérie, ser. 1, Paléont. no. 6, 1927.—*Bassani, Fr.*, Descrizione dei pesci fossili di Lesina accompagnata da appunti su alcune altre ittiofaune cretacee. Denkschr. k. Akad. Wiss. Wien, math.-naturw. Cl., vol. xlv., p. 195, 1882.—Aggiunte all' ittiofauna eocenica dei Monte Bolca e Postale. Palaeont. Ital., vol. iii., p. 77, 1897.—Ittiofauna delle argille plistoceniche di Taranto. Atti R. Accad. Sci. Napoli [2], vol. xii., no. 3, 1905.—*Cockerell, T. D. A.*, Cretaceous Fish Scales. U.S. Geol. Surv., Profess. Paper 120, 1919.—*D'Erasmo, G.*, l' ittiofauna fossile di Racalmuto. Giorn. Soc. Sci., etc., Palermo, vol. xxxv., p. 77, 1928.—L' ittiofauna fossile di Senigallia. Atti R. Accad. Sci. Napoli [2], vol. xviii., no. 1, 1929.—L' ittiofauna fossile del Gabbro. *Tom. cit.*, no. 6, 1930.—*Eastman, C. R.*, Les Types des poissons fossiles du Monte Bolca. Mém. Soc. Géol. France, vol. xiii., Paléont. no. 34, 1905.—Fishes from the Upper Eocene of Monte Bolca. Mem. Carnegie Mus., vol. iv., no. 7, 1911; vol. vi., no. 5, 1914.—*Hay, O. P.*, North American Cretaceous Actinopterous Fishes. Bull. Amer. Mus. Nat. Hist., vol. xix., art. 1, 1903.—*Jordan, D. S.*, Fish Fauna of the California Tertiary. Stanford Univ. Publ., Biol. Sci., vol. i., no. 4, 1921.—Fossil Fishes of Miocene of Southern California. *Loc. cit.*, vol. iv., no. 1, 1925.—*Jordan, D. S.*, and *Gilbert, J. Z.*, Fossil Fishes of Southern California. Leland Stanford Junior Univ. Publ., 1919.—Fossil Fishes of Diatom Beds of Lompoc, California. *Loc. cit.*, 1920.—*Kner, R.*, Über einige fossile Fische aus Kreide und Tertiärschichten von Comen und Podsused. Sitzungsb. k. Akad. Wiss. Wien, math.-naturw. Cl., vols. xlviii., lvi.—*Kner* and *Steindachner*, Neue Beiträge zur Kenntniss der fossilen Fische Österreichs. Denkschr. k. Akad. Wien, vol. xxi., 1863.—*Kramberger, D. G.*, Die eocänen Fische der Baschker Schichten. Palaeontogr., vol. xxiv., 1887.—Beiträge zur Kenntniss der fossilen Fische der Karpathen. Palaeontogr., vol. xxvi., p. 51, 1879.—Die jungtertiäre Fischfauna Kroatiens. Beitr. Paläont. u. Geol. Österr.-Ungarns, vols. ii., iii., 1882-83.—De piscibus fossilibus Comeni, Mrzleci, Lesinae, et M. Libanonis, etc. Djela Jugoslav. Akad., vol. xvi., p. 4, 1895.—*Meyer, H. von*, Palaeontogr., vols. ii., vi.—*Priem, F.*, Poissons fossiles de Perse. Mission de Morgan, Annales, 1908.—Poissons fossiles des terrains tertiaires d'eau douce et d'eau saumâtre de France et de Suisse. Mém. Soc. Géol. France, Paléont., no. 50, 1914.—*Sauvage, H. E.*, Bull. Soc. Géol. France, ser. 3, vols. ii, iii., vi., xi.—*Steindachner, F.*, Beiträge zur Kenntniss der fossilen Fischfauna Österreichs, i.-iv. Sitzungsb. k. Akad. Wien, vols. xxxvii., xxxviii., xl., xlvii., 1859-63.—*Weiler, W.*, Die mittel- und obereocäne Fischfauna Ägyptens mit besonderer Berücksichtigung der Teleostomi. Abhandl. Bay. Akad. Wiss., math.-naturwiss. Abt., n.s., 1, 1929.—*Wettstein, A.*, Über die Fischfauna des tertiären Glarnerschiefers. Abh. schweiz. paläont. Ges., vol. xiii., 1886.—*Lotz, L. F.*, Die Fische der typischen Fischschiefer aus den Schächten der Kaliwerke Buggingen. Mitt. Badisch. Geol. Landesanst., vol. x., p. 147, 1928.

internal skeleton is often characterised by its very dense structure and the sparse development of bone cells. The caudal fin, unlike that of the ganoids, is usually both internally and externally homocercal. In the more specialised forms the pelvic fins are sometimes displaced far forwards, while the rays of the dorsal and anal fins are sometimes articulated, sometimes spinous.

The *Teleostei* are divided here into the nine Orders of *Isospondyli*, *Ostariophysi*, *Haplomi*, *Apodes*, *Percesoces*, *Hemibranchii*, *Anacanthini*, *Heterosomata*, and *Acanthopterygii*. A more precise and detailed classification, such as has been elaborated during recent years for the existing bony fishes, cannot be applied to many of the crushed and fragmentary remains of extinct fishes. A large proportion of the identifications of the Tertiary Teleosteans, indeed, are at present unsatisfactory and uncertain. In the lower groups (*Physostomi*) the air bladder, when present, is connected by a tube with the oesophagus; in the more specialised groups (*Physoclysti*) there is no such connection in the adult fish.

A. PHYSOSTOMI.

Air bladder, when present, connected by a tube with the oesophagus.

Order 1. ISOSPONDYLI.

Symplectic bone present. No vertebrae fused or specially modified. Pectoral arch with precoracoid arch (or mesocoracoid). Pelvic fins abdominal; all fin rays articulated. Scales, when present, usually cycloid.

Of all the bony fishes the *Isospondyli* approach most closely the Ganoids, especially the *Protospondyli* and *Halecostomi*. They probably originated from the latter, becoming specialised in their own line, and soon considerably exceeding their ancestors in diversity of form. They already exhibit an important development in the Lower Cretaceous, but attain their widest distribution in the Tertiary and at the present day. They live partly in the sea, partly in fresh waters.

Family 1. Elopidae.[1]

Trunk fusiform, and caudal region relatively short. Supraoccipital bone not prominent, but extending forwards beneath the united parietals or separating the latter in the median line; squamosals suturally united with parietals and completely covering the otic bones except behind; well-developed cheek plates, not enamelled; jaws as in Clupeidae. *Opercular apparatus complete, with numerous branchiostegal rays, and usually a jugular plate. A single dorsal fin, without adipose dorsal. Scales thin and cycloid, without bony layer.* Cretaceous to Recent.

Elopopsis Heckel. Gape of mouth wide, with large teeth. *E. fenzli* Heckel, from Neocomian, Comen, Istria. *E. ziegleri* v. d. Marck, and other species in the Upper Cretaceous of Western Europe.

Osmeroides Ag. (*Rhabdolepis* v. d. Marck *nec* Troschel; *Holcolepis* v. d. Marck). Salmon-shaped fishes with minute clustered teeth, and very deeply overlapping scales. *O. lewesiensis* Mantell sp., from English Chalk. Other species in the Upper Cretaceous of Westphalia, Bohemia, and Mount Lebanon.

[1] *Ridewood, W. G.*, Cranial Osteology of *Elopidae* and *Albulidae*. Proc. Zool. Soc., 1904, vol. ii., p. 35.—Cranial Osteology of the Clupeoid Fishes. *Loc. cit.*, p. 448.

Flindersichthys Longman. Lower Cretaceous; Queensland.

Thrissopater Günther. Single series of small conical teeth on margin of jaws. Abdomen compressed to sharp edge. *T. salmoneus* Gthr. Gault; Folkestone. *Dinelops* A. S. Woodw. English Chalk.

Pachyrhizodus Dixon (*Hypsodon* Ag. p.p.; *Raphiosaurus* Owen; *Acrodontosaurus* Mason). Teeth stout and conical, not compressed, fused with supporting bone; premaxilla horizontally extended, with a row of marginal teeth and two larger teeth within. Vertebral centra deeper than long, not pitted at the sides. *P. basalis* Dixon; *P. latimentum* Cope. Upper Cretaceous; Europe and North America.

Rhacolepis Ag.; *Notelops* A. S. Woodw.; *Enneles* Jordan and Branner; *Ennelichthys*, *Brannerion* Jordan. Cretaceous; Ceará, Brazil.[1]

Protelops Laube. Upper Cretaceous; Bohemia.

Megalops Lacép.; *Elops* Linn. Eocene to Recent.

Esocelops A. S. Woodw. Lower Eocene; England.

Spaniodon Pictet. One or two pairs of large conical teeth near front end of mandible. Ribs very long, straight and slender. Dorsal fin opposite pelvic pair. *S. blondeli* Pict., from Upper Cretaceous, Sahel Alma, Lebanon. *S. simus* Cope. Upper Cretaceous; Dakota, U.S.A.

Thrissopteroides v. d. Marck. As *Spaniodon* but dorsal fin behind pelvic pair. Upper Cretaceous; Westphalia and Lebanon.

Brouweria de Beaufort. Miocene; S. Celebes.

Family 2. Albulidae.

Clupeoids with very small mouth, and some inner bones with grinding teeth. Branchiostegal rays few, and jugular plate absent. Upper Cretaceous to Recent.

Istieus Ag. (Fig. 238). An elongate fish, with much extended dorsal fin, small anal fin, and forked tail. Teeth very small. Closely resembling the

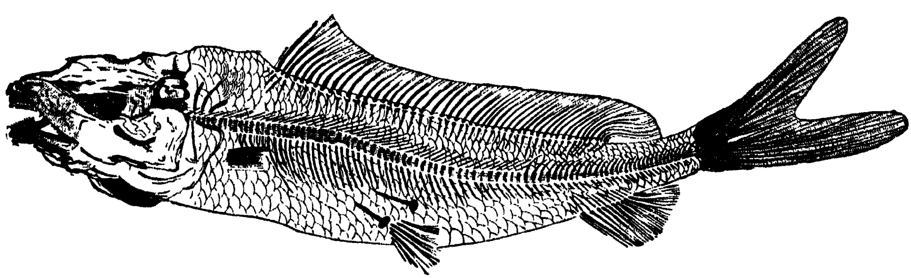


FIG. 238.

Istieus mesospondylus v. d. Marck. Upper Cretaceous; Sendenhorst, Westphalia. About 1/6 nat. size (after W. von der Marck).

existing deep-sea fish *Bathythrissa* Günther. About three species in the Upper Cretaceous of Westphalia and Lebanon.

Pisodus Owen. Large hemispherical or flattened crushing teeth on the parasphenoid. Closely resembling existing *Albula*. Lower and Middle Eocene of England and Belgium.

[1] *Jordan, D. S.*, Mon. Serv. Geol. e Mineral. Brasil, vol. iii., p. 32, 1923.

Chanoides A. S. Woodw. Few stout conical teeth. Upper Eocene; Monte Bolca.

Family 3. **Chanidae.**

Clupeoids with small, usually toothless mouth, and parietals meeting in middle line. Branchiostegal rays few, without jugular plate. Cretaceous to Recent.

Prochanos Bassani. Toothless. No enlarged scale at base of tail. *P. rectifrons* Bass. Neocomian; Lesina, Dalmatia.

Chanos Lacépède. Toothless. Enlarged scale at base of tail. Eocene to Recent.

Family 4. **Plethodontidae.**[1]

Head much resembling that of Osteoglossidae, *but external bones less thickened; dental plate on parasphenoid opposed to another on glossohyal.* Upper Cretaceous.

Plethodus Dixon. A single dental plate, consisting of vertical tubules of dentine, above and below. *P. expansus* Dixon. Albian to Senonian; S.E.

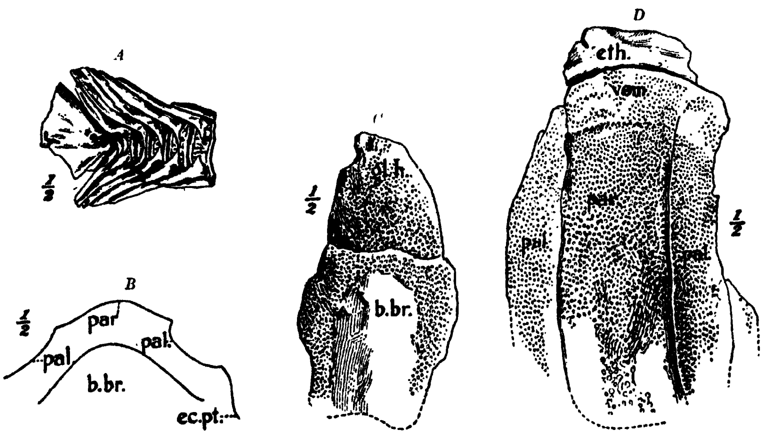


FIG. 239.

Anogmius aratus Cope. *A*, End caudal vertebrae. *B*, Transverse section across mouth. *b.br*, position of basibranchial; *ec.pt*, ectopterygoid; *pal*, palatine; *par*, parasphenoid. *C*, Basibranchial (*b.br.*) and glossohyal (*gl.h*) plates. *D*, Roof of palate. *eth*, ethmoid; *pal*, palatine; *par*, parasphenoid; *vom*, vomer. Chalk; Kansas. 1/2 nat. size (after Hay).

England. *P. furcatus* Fritsch sp. Turonian; Bohemia. Probably also in Egypt.

Anogmius Cope (Fig. 239). One median dental plate above, two median dental plates below. Marginal teeth minute and clustered. Body elongate-fusiform, and laterally compressed, with numerous short vertebrae. *A. aratus* Cope (Fig. 239), at least 1 m. in length. Upper Cretaceous (Niobrara Group): Kansas, U.S.A. *A. ornatus* A. S. Woodw. Lower Chalk; Lincolnshire.

Syntegmodus, Thryptodus, Pseudothryptodus Loomis. *Martinichthys* McClung, with elongated snout. Niobrara Group; Kansas, U.S.A.

[1] *Loomis, F. B.*, *Thryptodus*, etc. Palaeontogr., vol. xlvi., p. 229, 1900.—*Woodward, A. S.*, Cretaceous Fish *Plethodus*. Ann. Mag. Nat. Hist. [7], vol. iii., p. 353, 1899.—*Anogmius ornatus* sp. nov. The Naturalist, 1923, p. 297.

Chicolepis Cockerell. Scales from Cretaceous, Ortigalito Creek, California.
Kymatopetalolepis Cockerell. Scales from Turonian, Saxony.

Family 5. **Osteoglossidae.**

Head bones much thickened, and cheek plates robust; parietals meeting in middle line. Margin of upper jaw formed both by premaxilla and maxilla with teeth. Minute teeth clustered on parasphenoid and glossohyal. Scales large and thick, composed of mosaic-like pieces. Eocene to Recent.

Phareodus Leidy (*Dapedoglossus* Cope). Laterally compressed deep-bodied fishes from the Eocene Green River Shales of Wyoming, U.S.A.

Brychaetus A. S. Woodw. London Clay; Sheppey. Large skulls.

Scleropages Günther. Recent and in Tertiary, Sumatra.[1]

Osteoglossum and other genera are large freshwater fishes living in the tropics.

Family 6. **Ichthyodectidae.**[2]

Large extinct predaceous fishes, with a row of strong conical teeth fixed in sockets on the margin of the jaws. Upper jaw formed by short and deep premaxilla, and long stout maxilla; mandible deep, truncated in front, without any predentary bone. Vomer and parasphenoid toothless; palato-pterygoid arch with patches of small teeth. Paired fins composed of a very broad anterior, and numerous narrower rays, finely divided and articulated at the distal end. Dorsal fin short and remote; anal fin not much extended; caudal fin forked. Scales large, cycloid. Cretaceous.

FIG. 240.
Head of *Portheus molossus* Cope. Upper Cretaceous (Niobrara Group); Fox Cañon, Kansas. 1/4 nat. size (after Cope).

This family is closely related to the existing *Chirocentridae*, of which only one genus (*Chirocentrus*) is known, inhabiting the Indian Ocean. The latter may

[1] *de Beaufort, L. F.*, Osteoglosside Visch in het Tertiair van Sumatra. Verhand. Geol.-Mijn. Genootsch. Nederl. ed Kolon., Geol. Ser., vol. viii., p. 49, 1925.

[2] *Crook, A. R.* Über einige Knochenfische aus der mittleren Kreide von Kansas. Palaeontogr., vol. xxxix., p. 107, 1892.—*Loomis, F. B.*, Die Anatomie und die Verwandtschaft der Ganoid und Knochenfische aus der Kreide von Kansas. Palaeontogr., vol. xlvi., p. 213, 1900.—*McClung, C. E.*, Ichthyological Notes. Kansas Univ. Sci. Bull., vol. iv., p. 235, 1908.—*Osborn, H. F.*, *Portheus molossus* Cope. Bull. Amer. Mus. Nat. Hist., vol. xx., art. xxxi., 1904.—*Stewart, A.*, Teleosts of the Upper Cretaceous. Univ. Geol. Surv. Kansas, vol. vi., 1900.—*Woodward, A. S.*, New Specimen of *Portheus molossus* Cope. Geol. Mag. [5], vol. x., p. 529, 1913.

perhaps be represented by the extinct genus *Platinx* Ag. (*Thrissopterus* Heckel) in the Upper Eocene of Monte Bolca.

Portheus Cope (*Xiphactinus* Leidy; *Hypsodon* Ag. p.p.) (Fig. 240). Powerful fishes, sometimes 3 or 4 m. in length. Teeth of variable size, oval in transverse section. Palatine movably articulated with ethmoid, with hammer-shaped thickening. Eye with ossified sclerotic; three suborbital plates. Operculum well developed and large. *P. molossus* Cope (Fig. 240) and other species occur in the Chalk (Niobrara Group) of Kansas, U.S.A. *P. mantelli* Newton and other species in the Chalk and Gault of England, France, Belgium, Bohemia, and Saxony. Fragments also in Cretaceous of Rolling Downs, Queensland.

Spathodactylus Pictet. Much resembling *Portheus*. Neocomian; Voirons, Switzerland.

Ichthyodectes Cope. As *Portheus*, but smaller, and teeth of uniform size. Chalk of Kansas and England, perhaps also Queensland, Australia.

Gillicus Hay. Like the preceding, but teeth small and fringe-like. Upper Cretaceous; Kansas. Gault; Folkestone.

Chirocentrites Heckel. Lower Cretaceous; Istria.

Eubiodectes Hay. *E. libanicus* Pict. and Humb. sp. Upper Cretaceous; Hakel and Hajula, Lebanon.

Chiromystus Cope. Lower Cretaceous; Bahia, Brazil. ? Lower Eocene; Alagoas, Brazil.

Anaedopogon Cope. Upper Cretaceous; Ceará, Brazil.

Proportheus Jaekel. Cretaceous; Cameroons, Africa.

Scales of various *Ichthyodectidae* have been described as *Cladocyclus* Ag.

Family 7. **Saurodontidae.**

Skull laterally compressed; jaws powerful, as in Ichthyodectidae, *and bearing a single row of compressed, knife-like teeth, with nutrient foramina or notches below the internal alveolar border; toothless predentary bone present.* Cretaceous.

The two genera comprised in this family differ from the *Ichthyodectidae* in the presence of a predentary bone and in the form and manner of succession of the teeth.

Saurocephalus Harlan. Dental crowns low and much laterally compressed; nutritive foramina on the inner face of the jaw below the alveolar border. *S. lanciformis* Harlan. Upper Cretaceous; Kansas, U.S.A. *S. woodwardi* Davies. Danian; Maastricht, Holland.

Saurodon Hays (*Daptinus* Cope). Inner margin of each dental alveolus deeply notched. *S. leanus* Hays, and other species from Upper Cretaceous of New Jersey and Kansas, U.S.A. *S. intermedius* Newton. Chalk; Kent.

Family 8. **Clupeidae.** Herrings.

Trunk elegantly fusiform. Supraoccipital bone separating parietals, and otic region prominent; cheek plates reduced; premaxilla very small; maxilla large, entering the gape, with two supramaxillaries; dentition feeble. Opercular apparatus complete, but few branchiostegal rays, and no jugular plate. A single dorsal fin, nearly median, without adipose dorsal. Scales thin and cycloid, without bony layer. Lower Cretaceous to Recent.

Crossognathus Pictet. Head and trunk laterally compressed, with large deeply overlapping scales but no ventral ridge scutes. Preoperculum forming a great triangular expansion, and suboperculum relatively deep. Several anterior rays of dorsal fin undivided; pelvic fins opposite middle of dorsal; scales smooth and lateral line conspicuous. *C. sabaudianus* Pictet, about 35 cm. long, from Neocomian of Voirons, Switzerland, and Hanover.

Syllaemus Cope. Much resembling *Crossognathus*. Upper Cretaceous; Colorado, U.S.A., and England.

Pseudoberyx Pict. and Humb. No ventral ridge scutes. Scales pectinated. *P. syriacus* P. and H. Upper Cretaceous; Hakel, Mt. Lebanon.

Histiothrissa A. S. Woodw. No ventral ridge scutes. Fins relatively large. Scales smooth. *H. macrodactyla* v. d. Marck sp. Upper Cretaceous; Westphalia.

Halecopsis A. S. Woodw. Lower Eocene; Belgium and England.

Neohalecopsis Weiler. Oligocene; Flörsheim, Mainz.

Diplomystus Cope (*Copeichthys* Dollo; ? *Hyperlophus* Ogilby; *Histiurus* Costa; *Ellipes, Ellimma, Knightia* Jordan). Abdomen compressed to a sharp edge, and bordered with large ridge scutes; back between the occiput and dorsal fin armoured with smaller ridge scutes. *D. dentatus* Cope, and other species finely preserved in the Eocene Green River Shales of Wyoming, U.S.A. *D. goodi* Eastman, probably early Tertiary, Benito, Spanish Guinea, W. Africa. Smaller species in the Cretaceous of Mount Lebanon (*D. brevissimus* Blv. sp.), Italy, Istria, and Brazil; in the Lower Eocene of Alagoas, Brazil; in the Oligocene of the Isle of Wight; and in the Miocene of Sarkeui, Sea of Marmora. Closely allied fishes living in the rivers of New South Wales and Chile.

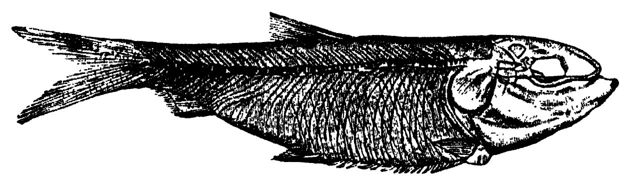


Fig. 241.
Clupea ventricosa H. v. Meyer. Lower Miocene; Unterkirchberg, near Ulm, Würtemberg. Nat. size.

Scombroclupea Kner. As *Clupea*, but finlets spaced out between the small anal and the forked caudal fin. *S. macrophthalma* Heckel sp. Upper Cretaceous; Mount Lebanon. Neocomian; Comen, Istria. Nearly similar fishes in the Cretaceous of Brazil. Perhaps also in Neocomian of Voirons, Switzerland.

Clupea Linn. (*Alosa* Cuv.). Herrings (Fig. 241). Abdomen compressed to a sharp edge, and bordered with large ridge scutes; no dorsal scutes. Teeth minute on the jaws and palatines, larger on the vomer and hyoid. Dorsal fin small and median. Not certainly known below the Upper Eocene of Monte Bolca, near Verona. Small species in the freshwater Lower Miocene of Unterkirchberg, near Ulm, Würtemberg. *C.* (*Sardinella*) *brouweri* de Beaufort. Miocene; South Celebes. Numerous Recent species.

Engraulis Cuv. Tertiary and Recent.

Etrumeus Bleeker. *E. boulei* Arambourg. Miocene; Licata, Sicily, and Oran, Algeria. Recent species.

Sahelinia Arambourg. Miocene; Oran, Algeria.

Meletta Val. (Fig. 242). Small slender fishes with scales marked with three to six pairs of radiating grooves. Jaws toothless. Ventral ridge scutes

large. Tertiary and Recent. Very common in the Lower Oligocene (Meletta-schiefer) of the Carpathians, Roumania, Croatia, Switzerland, Alsace, etc.[1]

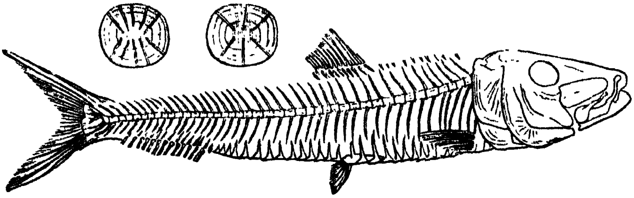


FIG. 242.
Meletta sardinites Heckel. Lower Oligocene; Radoboj, Croatia. Nat. size, with scales enlarged (after Heckel).

Dastilbe Jordan. Lower Eocene; Alagoas, Brazil.

Xyne Jordan. Found in shoals in Diatomaceous Earth, Santa Barbara Co., California.

Iquius Jordan. Tertiary; Japan.

Family 9. **Ctenothrissidae.**

Closely resembling Clupeidae, *but parietals partly meeting in middle line, and enlarged pelvic fins far forwards.* Upper Cretaceous.

Ctenothrissa A. S. Woodw. (Fig. 243). Scales ctenoid. *C. vexillifer* Pict.

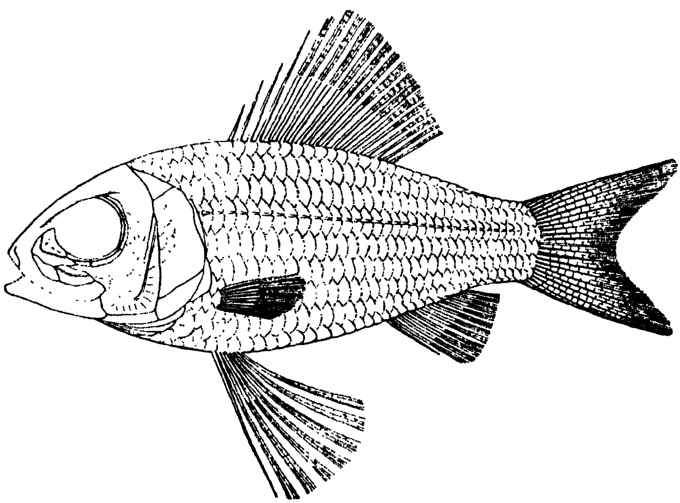


FIG. 243.
Ctenothrissa microcephala Ag. sp. Restoration by A. S. Woodward, about $1/2$ nat. size. English Chalk.

sp. Upper Cretaceous; Mount Lebanon. *C. radians, microcephala* Ag. sp. English Chalk.

Aulolepis Ag. Scales cycloid. English Chalk.

Family 10. **Salmonidae.** Salmon.

As Clupeidae, *but a small adipose fin behind the dorsal fin.* Upper Tertiary and Recent.

Thaumaturus Reuss and *Prothymallus* Laube. Miocene; Bohemia.

[1] *Weiler, W.*, Das Vorkommen isolierter Köpfe bei fossilen Clupeiden. Senckenbergiana, vol. xi., p. 40, 1929.

Salmo Linn. Doubtfully recorded from the Lower Miocene of Bohemia and the Upper Miocene of Croatia.

Fossil skeletons of the existing *Mallotus villosus* Müll. are very common in nodules in Pleistocene Clay on the coast of Greenland and in the glacial deposits of Canada. They have also been found at a height of 580 m. in S. E. Bosnia.[1]

Order 2. OSTARIOPHYSI.

As Isospondyli, *but some anterior vertebrae fused together, and air bladder connected with organs of hearing by a chain of ossicles.*

Family 1. **Characinidae.**[2]

Freshwater fishes with cycloid scales. Maxilla usually entering upper margin of mouth; teeth usually on margin of jaws, and lower pharyngeals not falciform; no barbels. Usually an adipose dorsal fin. Upper Tertiary and Recent.

Numerous in the freshwaters of tropical Africa and America. *Eobrycon* Jordan and *Lignobrycon* Eigenmann and Myers occurring in a lignite at Taubaté, San Paulo, Brazil. *Myletes* Cuvier, in the Tertiary of Iquitos, Loreto, Peru.

Characilepis Cockerell. Scales from Miocene of Huacho, Peru.

Family 2. **Cyprinidae.** Carps, etc.

Freshwater fishes with cycloid scales. Premaxilla excluding maxilla from upper margin of mouth; barbels present or absent. Mouth toothless, but lower pharyngeals falciform and bearing one to three rows of hollow prehensile teeth. Usually only three branchiostegal rays. Tertiary and Recent.

The Cyprinoids are numerous in the freshwaters of the Old World and North America, but do not occur in South America. Most of the known fossil species, all from freshwater formations, belong to the existing genera *Leuciscus* Klein[3] (Fig. 244), *Tinca, Gobio, Barbus* Cuv., *Rhodeus, Aspius* Ag. (Fig. 245), *Cyprinus, Cobitis* (Artedi) Linn., *Nemachilus* Cuv., *Thynnichthys* Bleeker, etc. *Blicca* Heckel is perhaps represented by a fragment from the Lower Eocene of Croydon, Surrey. The only extinct genera, such as *Amyzon, Diastichus, Oligobelus* Cope, *Mylocyprinus* Leidy, *Daunichthys* Annan-

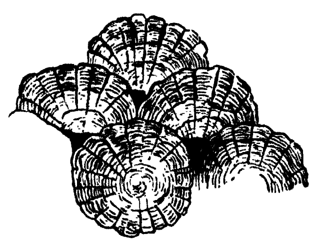


Fig. 244.
Scales of *Leuciscus oeningensis* Ag. Upper Miocene; Oeningen, Baden. Enlarged (after Winkler).

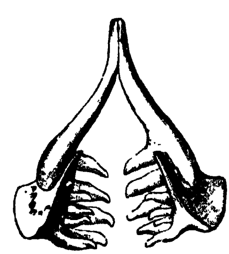


Fig. 245.
Pharyngeal bones and teeth of *Aspius rapax* Ag. Recent (after Heckel and Kner).

[1] *Bolkay, St. J.*, Novitates Musei Sarajevoensis, no. 3, 1925.
[2] *Eigenmann, C. H.*, and *Myers, G. S.*, The Fossil Characins. Mem. Mus. Comp. Zool. Harvard, vol. xliii., p. 512, 1929.
[3] *Royo y Gómez, J.*, Los Peces fósiles de los Aljezares de Teruel. R. Soc. Espan. Hist. Nat., vol. of 50th anniv., p. 19, 1921.

dale and Hora,[1] and others are closely related to existing forms. *Capitodus* and *Soricidens* Münster are names given to pharyngeal teeth from the Middle Miocene of Vienna.

Family 3. **Siluridae.**[2] (*Nematognathi.*) Cat-fishes.

Scaleless fishes, naked or armoured with bony plates. Premaxilla excluding maxilla from upper margin of mouth, the rudimentary maxilla usually supporting a barbel. Suboperculum absent. Postcleithral plates present. Anterior pectoral fin ray usually a strong bony spine. Eocene to Recent.

The Siluroids form a very numerous family of freshwater fishes, ranging over all temperate and tropical regions, and a few sometimes passing into the sea round the coasts. Fossil remains are rare, and represent fishes closely resembling those still surviving. The oldest known fragment is a portion of head (*Bucklandium diluvii* König) from the London Clay of Sheppey. Typical remains of *Arius* occur in the Middle and Upper Eocene of the Hampshire Basin, Belgium, Egypt, and Nigeria. Skulls of *Chrysichthys* are known from the Middle Eocene of Ameki, Nigeria. Other genera are recorded from the Eocene of Wyoming, U.S.A. (*Rhineastes* Cope) and Egypt (*Fajumia*, *Socnopaea* Stromer; *Ariopsis* Peyer), the Lower Pliocene of the Siwalik Hills, India, and Tertiary Lignites near Padang, Sumatra, and Taubaté, San Paulo, Brazil. *Corydoras* is found in the Upper Tertiary of Sunchal, Jujuy, Argentina (Cockerell, Science, vol. lxii., p. 397, 1925). *Silurus* occurs in the Pliocene and Pleistocene of Hungary. Numerous fragments in the late Tertiary formations of Africa and South America.

Order 3. HAPLOMI.

As Isospondyli, *but no precoracoid arch (or mesocoracoid) in the pectoral arch.*

Family 1. **Dercetidae.** (*Hoplopleuridae* Pictet p.p.)

Eel-shaped fishes with pectoral and pelvic fins, a more or less extended dorsal fin, and separate anal and caudal fins. Parietal bones large and in contact mesially; premaxilla forming margin of upper jaw. Vertebral centra as delicate cylinders, with parapophyses bearing the ribs. No overlapping scales; but paired longitudinal series of bony scutes. Cretaceous.

Dercetis Agassiz. Snout elongated and pointed; teeth minute and clustered. Dorsal fin occupying greater part of back, and pelvic fins inserted opposite to it; anal fin short, opposite hinder end of dorsal; caudal fin forked. Dermal scutes more or less angulated and ornamented with tubercles or spines; two dorsal series, two ventral series, and a paired series supporting the lateral line. *D. scutatus* Ag. Upper Cretaceous; Westphalia. *D. maximus* A. S. Woodw. Upper Chalk; Grays, Essex.

[1] *Annandale, N.*, and *Hora, S. L.*, Freshwater Fish from the Oil Measures of the Dawna Hills. Rec. Geol. Surv. India, vol. lvi., p. 204, 1925.

[2] *Leiderfrost, J.*, Die fossilen Siluriden Ungarns. Mitt. Jahrb. k. ung. Geol. Anst., vol. xxiv., p. 117, 1925.—*Neumayer, L.*, Zur vergleichenden Anatomie des Schädels eocäner und rezenter Siluriden. Palaeontogr., vol. lix., p. 251, 1912.—*Peyer, B.*, Die Welse des ägyptischen Alttertiärs nebst einer kritischen Übersicht über alle fossilen Welse. Abhandl. Bay. Akad. Wiss., math.-naturwiss. Abt., n.s., vol. xxxii., no. 3, 1928.—*Priem, F.*, Mém. Soc. Géol. France, Paléont. no. 49, 1914.—*Stromer, E.*, Nematognathi aus dem Fajûm und dem Natrontale. Neues Jahrb. f. Min., etc., 1904, vol. i., p. 1.

Leptotrachelus W. v. d. Marck (*Triaenaspis* Cope). As *Dercetis*, but dorsal fin not occupying more than middle third of back, and anal fin behind it. *L. triqueter* Pict. sp. and other species from the Cretaceous of the Lebanon, Westphalia, and South Dakota, U.S.A. *L. elongatus* Ag. sp., from English Chalk. A swallowed fish in a distended stomach is seen in some specimens from the Lebanon.

Pelargorhynchus v. d. Marck. With small scales between the scutes. Upper Cretaceous; Westphalia.

Stratodus Cope. Premaxilla short, with several rows of teeth; palatine and mandibular teeth large, numerous, in several rows, all with pulp cavity. Upper Cretaceous; Kansas.

To the existing **Stomiatidae** of the genera *Gonostoma* Rafinesque and *Photichthys* Hutton, Arambourg refers some species from the Miocene of Licata, Sicily, and Oran, Algeria. *Tomognathus* Dixon, with much extended dorsal fin, from the English Chalk, seems to be related to the same family.

Family 2. **Halosauridae.**

Eel-shaped fishes with pectoral and pelvic fins, a short dorsal fin, an extended anal fin usually confluent with the diminutive caudal, and both head and trunk covered with cycloid scales. Margin of upper jaw formed by both premaxilla and maxilla. Vertebral centra as delicate cylinders. Lateral line with luminous organs along the ventral border of the flank. Upper Cretaceous to Recent.

Halosaurus Johnson, living at great depths in the ocean. *Echidnocephalus* W. von der Marck,[1] an almost identical genus from the Upper Cretaceous of Sendenhorst, Westphalia.

Enchelurus v. d. Marck. With separate caudal fin. *E. villosus* v. d. Marck. Upper Cretaceous; Westphalia. Other species from Upper Cretaceous of Mt. Lebanon and England.

Family 3. **Notacanthidae.**

Eel-shaped fishes with or without a diminutive caudal fin. Premaxilla forming margin of upper jaw. Parietal bones partly in contact mesially. Pectoral arch connected with skull by ligament; pelvic fins far back; dorsal fin rudimentary, much extended, usually with widely spaced undivided rays. Cretaceous to Recent.

Pronotacanthus A. S. Woodw. With dorsal fin supports but no rays. Upper Cretaceous; Sahel Alma, Mount Lebanon.

Notacanthus Bloch. In existing deep sea.

Family 4. **Enchodontidae.** (*Hoplopleuridae* Pictet p.p.)

Rapacious fishes with more or less fusiform trunk. Parietal bones very small, separated by the supraoccipital; delicate premaxilla extended and nearly excluding the rod-like maxilla from the margin of the upper jaw, which bears small teeth; powerful teeth fused with the palato-pterygoid and dentary bones. Vertebral centra robust, none with parapophyses. A small adipose fin probably present behind the single dorsal fin. A median series of dorsal bony scutes, and often a paired series of similar scutes supporting the lateral line; scales very small or absent. Cretaceous.

[1] *Woodward, A. S.*, Proc. Zool. Soc., 1897, p. 268.

Enchodus Ag. (*Eurygnathus* Davis; *Ischyrocephalus* v. d. Marck; *Solenodon, Holcodon* Kramb.) (Fig. 246). The largest and longest tooth at the anterior end of the palatine; large teeth of dentary spaced, increasing in length to the symphysis. External bones more or less tuberculated. Three or four oval median scutes between the occiput and dorsal fin; an adipose dorsal on

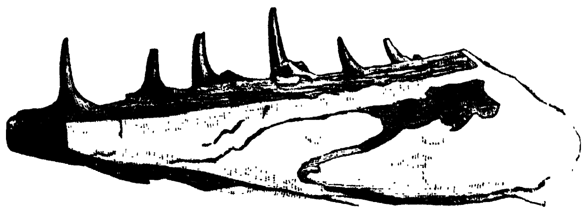


FIG. 246.
Imperfect dentary bone of *Enchodus lewesiensis* Mant. sp. Lower Chalk; Lewes. Nat. size (after Agassiz).

the tail; caudal fin forked. No postcleithral plate; no scutes along course of lateral line, but a recurved hooklet on each side of the caudal pedicle. *E. lewesiensis* Mant. sp., from the Chalk of S.-E. England. Well-preserved skeletons of other species in the Cretaceous of Westphalia, Istria, and the Lebanon. Fragments in the Upper Cretaceous of North and South America, and Maastricht Beds, Holland.

Palaeolycus W. von der Marck. As *Enchodus*, but dorsal opposed to extended anal fin, not in advance. *P. dreginensis* v. d. M., from Upper Cretaceous, Westphalia.

Eurypholis Pictet (Fig. 247). As *Enchodus*, but a large postcleithral plate, and well-developed scutes along the course of the lateral line. *E.*

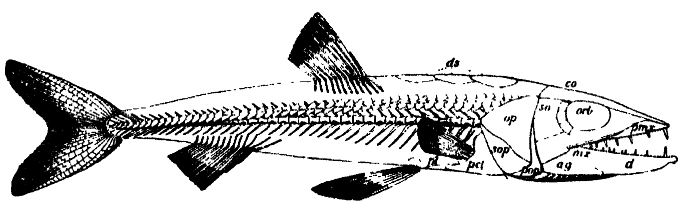


FIG. 247.
Eurypholis boissieri Pictet. Restoration by A. S. Woodward, about $1/2$ nat. size. Upper Cretaceous; Hakel, Mount Lebanon. *ag*, angular; *co*, circumorbitals; *d*, dentary; *ds*, dorsal scutes; *mx*, maxilla; *op*, operculum; *orb*, orbit; *pcl*, postcleithral plate; *pl*, pelvic fin support; *pmx*, premaxilla; *pop*, preoperculum; *so*, suborbitals; *sop*, suboperculum.

boissieri Pictet (Fig. 247), from Upper Cretaceous of Hakel and Hajula, Mount Lebanon.

Saurorhamphus Heckel.[1] As *Eurypholis*, but more elongated, with slender snout, and more remote dorsal fin. *S. freyeri* Heck. Neocomian; Comen, Istria.

Cimolichthys Leidy (*Plinthophorus* Günther; *Empo* Cope). Largest teeth in middle of palato-pterygoid arcade semi-barbed at apex. Clustered teeth in mandible, with simply pointed larger teeth at intervals. *C. lewesiensis* Leidy, from Chalk of S.-E. England. *C. nepaeolica* Cope sp. and other species in Niobrara Cretaceous of Kansas, U.S.A.

[1] *D'Erasmo, G.*, Boll. Soc. Adriatica Sci. Nat., Trieste, vol. xxvi., p. 45, 1912.

Prionolepis Egert. (*Aspidopleurus* Pict. and Humb.; *Apateopholis* A. S. Woodw.); *Leptecodon* Williston. Upper Cretaceous.

Halec Ag. (*Pomognathus* Dixon; *Archaeogadus* v. d. Marck; *Phylactocephalus* Davis). Premaxilla very slender, with minute teeth; maxilla equally slender, with a few relatively large spaced teeth at its hinder end. Palato-pterygoid teeth closely arranged, laterally compressed cones, largest in the middle of the arcade. No dermal scutes, except a pair of recurved hooklets on the caudal pedicle. *H. eupterygius* Dixon sp., well preserved in Lower Chalk, S.-E. England. *H. sternbergi* Ag., in Turonian, Bohemia. *H. microlepis* Davis sp., showing minute quadrangular scales, in Upper Cretaceous, Hakel and Hajula, Mount Lebanon. Other species in Cretaceous, Isle of Lesina, Dalmatia.

Halecodon Cockerell. Cretaceous; Wyoming, U.S.A.

Apateodus A. S. Woodw. Premaxilla and maxilla very slender. Palatine elongated and pointed in front; large laterally compressed teeth largest in middle of palato-pterygoid arcade; small recurved teeth in front of mandible. *A. striatus* A. S. Woodw. English Chalk. *A. corneti* Forir sp.,[1] from Senonian, Limburg.

? *Pantopholis* Davis. Upper Cretaceous; Sahel Alma, Mount Lebanon.

Family 5. **Scopelidae.** (*Myctophidae.*)

Premaxilla much extended, excluding maxilla from upper margin of mouth. Skull and skeleton as in Enchodontidae. *A small adipose fin behind the dorsal fin. No air bladder. Trunk naked or scaly, without bony scutes.* Cretaceous to Recent.

Exclusively marine fishes, for the most part pelagic or deep-sea forms.

Sardinioides v. d. Marck (Fig. 248). Teeth minute; maxilla expanded behind. Dorsal fin median; pectoral fins small; caudal fin slightly forked.

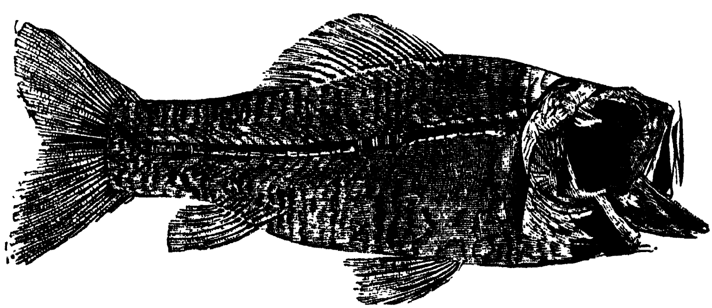


FIG. 248.
Sardinioides monasteri Ag. sp. Upper Cretaceous; Sendenhorst, Westphalia. 1/2 nat. size.

Scales large, serrated at the hinder border. *S. monasteri* Ag. sp. (Fig. 248), from Upper Cretaceous, Sendenhorst, Westphalia. Other species from Mount Lebanon and England.

Leptosomus v. d. Marck. Relatively small species, as *Sardinioides* but paired fins nearly equal in size and scales cycloid. Upper Cretaceous; Westphalia and Mount Lebanon.

[1] *Kruizinga, P.*, Proc. R. Acad. Sci. Amsterdam, vol. xxvii., p. 293, 1924.

Sardinius v. d. Marck. Upper Cretaceous; Westphalia. *Acrognathus* Ag. Upper Cretaceous; England and Mount Lebanon. *Opisthopteryx* Pictet and Humb. Upper Cretaceous; Mount Lebanon.

Nematonotus A. S. Woodw. One dorsal and one pectoral fin ray elongated and tactile. Upper Cretaceous; Hakel and Hajula, Mount Lebanon.

Microcoelia v. d. Marck. Back between occiput and dorsal fin with small thickened ridge scales. Upper Cretaceous; Westphalia and Mount Lebanon.

Dactylopogon v. d. Marck. First ray of pectoral fins elongated and tactile. *D. grandis* v. d. M. Upper Cretaceous; Sendenhorst, Westphalia.

Rhinellus Ag. (*Ichthyotringa* Cope) (Fig. 249). Slender fishes with very large pectoral fins, and the premaxillae produced forwards into a long pointed

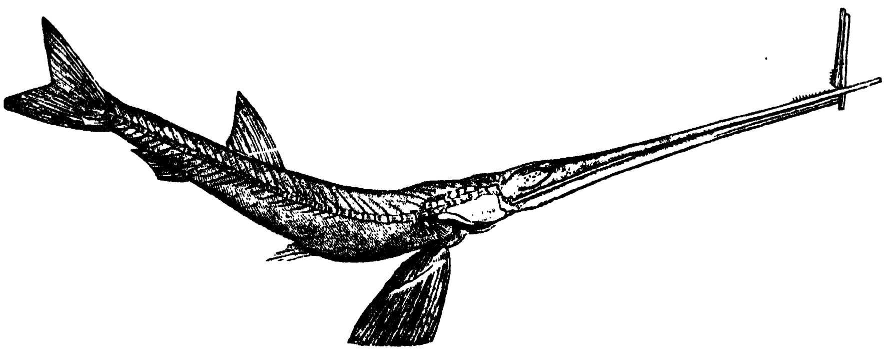


FIG. 249.

Rhinellus furcatus Ag. Upper Cretaceous; Sendenhorst, Westphalia (after W. v. d. Marck).

rostrum. Teeth slender and pointed. Dorsal fin small, in advance of the still smaller anal fin; caudal fin forked. Scales smooth, slightly enlarged along the course of the lateral line. Upper Cretaceous; Westphalia, Mount Lebanon, and South Dakota.

Scopeloides Wettstein. Oligocene; Canton Glarus.

Parascopelus Sauvage; *Paralepis*, *Scopelus* Cuvier (*Myctophum* Rafinesque); *Sudis* Raf. Miocene; Licata, Sicily; Gabbro, Leghorn; and Oran, Algeria.

? *Holosteus* Ag. Upper Eocene: Monte Bolca, Verona.

Family 6. **Gonorhynchidae.**[1]

Premaxilla smaller than maxilla, but excluding latter from margin of upper jaw. No adipose dorsal fin. No air bladder. Scales deeply overlapping, fringed behind with short spines. Cretaceous to Recent.

Charitosomus W. v. d. Marck (*Solenognathus* Pict. and Humb.). Scales not covering head. Upper Cretaceous; Westphalia and Mount Lebanon.

Gonorhynchops Cockerell. Scale from English Chalk.

Notogoneus Cope (*Sphenolepis* Ag.; *Protocatostomus* Whitfield). Scales covering head. Freshwater Eocene (Green River Shales); Wyoming, U.S.A. Upper Eocene and Oligocene; France and Germany.

Gonorhynchus Gronov. Existing in seas off Japan, S. Africa, Australia, and New Zealand.

[1] *Woodward, A. S.*, Extinct Fishes of the Teleostean family *Gonorhynchidae*. Proc. Zool. Soc., 1896, p. 500.

Family 7. **Chirothricidae.**[1]

Scopeloids with one pair of fins much enlarged, and pelvic fins far forwards. Abdominal vertebrae with parapophyses. Cretaceous.

Chirothrix Pictet and Humbert (*Megapus* Schlüter; *Megistopus* Landois). Branchiostegal rays very large, eight or nine in number. Pectoral fins comparatively small and delicate, with only one ray considerably elongated; the enlarged pelvic fins close to the pectorals, with about seventeen rays; dorsal fin deep, arising immediately behind the head; anal fin small; caudal fin forked. *C. libanicus* P. and H., from Upper Cretaceous, Mount Lebanon. *C. guestphalicus* Schlüter sp., from Westphalia.

Telepholis v. d. Marck. Upper Cretaceous; Westphalia and Mount Lebanon.

Exocoetoides Davis. Upper Cretaceous; Mount Lebanon.

Family 8. **Esocidae.** Pikes.

Trunk elongated, with large cycloid scales. Premaxilla and maxilla entering upper border of mouth. Premaxilla, mandible, palatine, and vomer with stout, pointed teeth; maxilla toothless. Dorsal fin remote. Upper Oligocene to Recent.

Fine specimens referable to the existing genus *Esox* Linn. occur at Oeningen and in other Miocene freshwater formations in Europe. Also Upper Oligocene Lignite of Rott, near Bonn.

Family 9. **Cyprinodontidae.**[2] Toothed carps.

Small freshwater fishes with cycloid scales. Premaxilla excluding maxilla from upper margin of mouth; no barbels. Margin of jaws and pharyngeal bones with pointed teeth. No anterior vertebrae fused. No adipose dorsal fin. Tertiary and Recent.

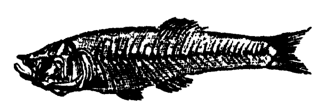


FIG. 250.

Prolebias meyeri Ag. sp. Litorinella-clay; Frankfurt-a.-M. Nat. size.

Of the genera of this family, *Prolebias* Sauvage (Fig. 250), allied to *Lebias* Cuv., is remarkably common in the Oligocene and Miocene of Europe. *P. cephalotes* Ag. sp. occurs in shoals in the Lower Oligocene of Aix-en-Provence.

Pachylebias A. S. Woodw. (*Aelia*, *Physocephalus* Costa). Upper Miocene; Italy, Sicily, and Crete.

Brachylebias Priem. Miocene; Lake Urmiah, Persia.

Gephyrura Cope. Lower Tertiary; Ree Hills, S. Dakota.

Parafundulus Eastman. Pleistocene (Lahontan Beds); Hazen, Nevada, U.S.A.

Carrionellus White. Lower Tertiary; Loja, Ecuador.

Order 4. APODES. Eels.

Body much elongated, cylindrical or ribbon-shaped. Premaxillae absent or fused with ethmoid and vomer; upper jaw formed laterally by the toothed maxilla. Dorsal

[1] *Landois, H.*, Die Familie Megistopodes. Neues Jahrb. f. Min., etc., 1894, vol. ii., p. 228.

[2] *White, E. I.*, Fossil Cyprinodont from Ecuador. Ann. Mag. Nat. Hist. [9], vol. xx., p. 519, 1927.

fin much extended, often meeting the anal round the tail. Pectoral arch not suspended from the cranium. Skin naked, or with small, rudimentary, cycloid scales.

Family 1. **Urenchelyidae.**

Caudal fin separate; one or both pairs of fins. Upper Cretaceous.

Urenchelys A. S. Woodw. Without pelvic fins. Caudal fin rounded. Upper Cretaceous; Mount Lebanon, Sweden, and English Chalk.

Anguillavus Hay. With very small pelvic fins. Upper Cretaceous; Hajula, Mount Lebanon.

The existing *Anguillichthys* Mowbray (Bull. Bingham Oceanographic Collection, vol. i., art. 1, p. 10, 1927), belonging to a distinct family, has a slightly forked caudal fin and comparatively short median fins, probably a secondary adaptation to oceanic life.

Family 2. **Anguillidae.**

Caudal fin absent or confluent with dorsal and anal fins. No pelvic fins. Tertiary and Recent.

Mylomyrus A. S. Woodw. A primitive eel with large crushing teeth, large supracleithrum, well-developed hypural bones, and extensive squamation. *M. frangens* A. S. W. Eocene of Egypt.

Rhynchorhinus A. S. Woodw. Lower Eocene (London Clay); Sheppey.

Eomyrus Storms. Middle Eocene; Belgium. Upper Eocene; Monte Bolca.

Nemichthys Richardson. ? *N. mecquenemi* Priem. Eocene; Persia.

Paranguilla Bleeker (*Enchelyopus* Ag.). Upper Eocene; Monte Bolca.

Anguilla Shaw; *Nettastoma* Rafinesque. Also supposed to occur in Upper Eocene of Monte Bolca.

Mastygocercus de Beaufort. Miocene; South Celebes.

Species of existing genera from freshwater Oligocene of Aix-en-Provence, and Upper Miocene, Oeningen.

B. PHYSOCLYSTI.

Air bladder, when present, not connected by a tube with the oesophagus in the adult (except in certain Berycidae).

Order 5. PERCESOCES.

As Haplomi, *but physoclystous and the dorsal fin often with a spinous portion in front. Pelvic fins always abdominal.*

Family 1. **Scombresocidae.**

Premaxilla and maxilla forming margin of upper jaw. Lower pharyngeal bones united. Pectoral fins sometimes much enlarged, wing-like; pelvic fins without spine; dorsal fin remote, opposite the anal fin; all fin rays articulated and flexible. Scales cycloid. Miocene to Recent.

Extinct species of *Belone* Cuv. and *Scombresox* Lacép. are known from the Miocene of Europe and Algeria.

Cobitopsis Pomel. Freshwater Oligocene; Puy-de-Dôme, France.

Family 2. **Atherinidae.**

Premaxilla excluding maxilla from margin of upper jaw. Dentition feeble. Lower pharyngeal bones separate. Pelvic fins with one spine and five divided rays; a separate anterior spinous dorsal fin. Eocene to Recent.

Atherina Linn. Extinct species from Upper Eocene of Monte Bolca, Italy, and Gard, France, and from Upper Miocene of Dolje, Croatia.
Rhamphognathus Ag. (*Mesogaster* Ag.). Upper Eocene; Monte Bolca.

Family 3. **Mugilidae.**

As Atherinidae *but with mouth protractile and pelvic fins further forwards.* Oligocene to Recent.

Mugil Linn. Extinct species in Oligocene of Aix-en-Provence and Miocene of Croatia and Algeria.

Family 4. **Sphyraenidae.**

Premaxilla excluding maxilla from margin of upper jaw; mouth large, with large pointed teeth in sockets. Fins as in Atherinidae. Eocene to Recent.

Sphyraena Artedi. Extinct species in Upper Eocene, Monte Bolca; Oligocene, Austria; and Miocene, Italy, Croatia, and South Celebes. Teeth in other Tertiary formations in Europe, Egypt, Nigeria, and America.

Order 6. HEMIBRANCHII.

Anterior vertebrae modified or coalesced. Branchial arches more or less reduced. Pelvic fins usually abdominal; dorsal fin sometimes with a spinous portion in front.

The most generalised family **Gasterosteidae** (Sticklebacks) is not represented among fossils, except in the Pleistocene of North America.

Family 1. **Aulorhynchidae.**

Elongated marine fishes, with elongated tube-shaped snout and remote dorsal fin. Anterior vertebrae slightly elongated. Pelvic and anal fins with a spine; free dorsal fin spines. Rows of small bony dermal plates. Eocene to Recent.

Protaulopsis A. S. Woodw. Upper Eocene; Monte Bolca.
Aulorhynchus Gill (*Protosyngnathus* W. v. d. Marck). Recent in Pacific Ocean. *A. sumatrensis* v. d. Marck sp. Tertiary; Padang, Sumatra.

Family 2. **Aulostomidae.** Flute-mouths.

Elongated marine fishes, with elongated tube-shaped snout and remote dorsal fin. Occiput movably articulated with the vertebral column, of which the first four vertebrae are elongated and fused together; teeth small. Spines little developed. Pelvic fins abdominal or thoracic. Scales small or absent. Eocene to Recent.

Fistularia Linn., and *Aulostoma* Lacép., and the extinct genus *Urosphen* Ag., occur in the Upper Eocene of Monte Bolca. *Aulostoma media* Weiler, in the

Oligocene, Mainz. *Fistularia koenigi* Ag., in the Oligocene, Glarus, Switzerland; other species in Miocene of Licata, Sicily, and Gabbro, Leghorn.

Family 3. **Centriscidae.**

Trunk laterally compressed, irregularly oblong or deepened; snout elongated and tube-shaped. Some anterior vertebrae elongated. Pelvic and anal fins without spine; dorsal fin with few spines, one being excessively enlarged. Scales usually present, and bony scutes dorsally and usually ventrally. Eocene to Recent.

Centriscus Linn. Recent. Perhaps spines in Lower Pliocene of Orciano, Tuscany.

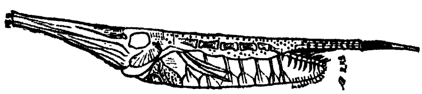


Fig. 251.
Amphisyle heinrichsi Heckel. Lower Oligocene; Krakowiza, Carpathians. Nat. size (after Heckel).

Rhamphosus Ag. Bony plates dorsally, not ventrally, and flanks covered with small scales. Upper Eocene; Monte Bolca.

Amphisyle (Klein) Cuv. (Fig. 251). Recent in Indian and Pacific Oceans. Fossil in the Oligocene Menilite shales of Galicia, Vienna basin, Alsace, Mainz, and Switzerland.

Families 4, 5. **Solenostomidae and Syngnathidae.** Pipe-fishes, etc.

Gills arranged in tufts on the branchial arches and protected by an operculum. Snout with tubular extension, and jaws toothless. Pelvic fins, often also the anal and caudal fins, wanting. Skin armoured with thin bony plates. Eocene to Recent.

Only very few fossil representatives of these two families are known. The elongated **Solenostomidae**, in which all the fins are developed, have an Eocene forerunner in the genus *Solenorhynchus* Heckel from Monte Postale. Extinct species of *Siphonostoma*, which is still common in the Mediterranean, also occur in the Miocene of Licata, Sicily (Fig. 252), and of Tuscany.

Fig. 252.
Siphonostoma albyi Sauvage. Miocene; Licata, Sicily (after Sauvage).

Several Tertiary forms of **Syngnathidae** are known; *Syngnathus*, *Pseudosyngnathus*, and an extinct genus *Calamostoma* Ag., occur in the Eocene. *Calamostoma* is related to *Hippocampus* Raf., but has a caudal fin.

Order 7. ANACANTHINI.

Parietal bones separated by supraoccipital. Air bladder present. All fin rays flexible and articulated. Pelvic fins jugular or thoracic, usually with more than six rays; pelvic bones not in direct contact with pectoral arch. No homocercal caudal fin, but hindmost vertebrae progressively smaller.

Family 1. **Gadidae.** Cod-fishes.

Elongated fishes with broad head, and the toothed premaxilla excluding the maxilla from the upper margin of the mouth. Pelvic fins jugular. Dorsal fin

extending almost the whole length of the back, sometimes subdivided into two or three parts ; anal fin much extended, sometimes divided into two. Scales small and smooth. Eocene to Recent.

Fossil representatives of this family are rare. An extinct genus, *Nemopteryx* Ag. (*Palaeobrosmius*, *Palaeogadus* vom Rath) occurs in the Oligocene

FIG. 253.
Merluccius emarginatus Koken. Otoliths, four (*A*) and three (*B*) times nat. size. Upper Oligocene ; Germany (after Koken).

slates of Canton Glarus. Remains of *Phycis*, *Strinsia*, *Gadus*, *Bregmaceros* (*Podopteryx* Sauvage), and *Brosmius* have been described from the Miocene of Hungary, Croatia, Sicily, and Algeria. Small fishes ascribed to *Gadus* are found in nodules in the Glacial clay, Bindalen, Norway. Numerous otoliths (*e.g.* Fig. 253) occur in various Tertiary formations, including the Pliocene Crags of East Anglia. Undetermined skulls are known from the London Clay of Sheppey.

FIG. 254.
Macrurus sp. Otolith, twice nat. size. Pliocene ; Orciano, near Pisa.

Otoliths apparently referable to genera of the allied family **Macruridae** (Fig. 254) occur in Oligocene and later Tertiary formations. *Trichiurichthys* Sauvage, from the Miocene of Licata, Sicily, may also be Macrurid.

Otoliths of **Ophidiidae** occur in the Upper Eocene of Barton, Hampshire (*Neobythites* Goode and Bean and *Fierasfer* Cuvier), and in the Oligocene of Germany.

Order 8. HETEROSOMATA.

Skull asymmetrical in adult, with both eyes on one side of head. Parietal bones separated by supraoccipital. Air bladder absent in adult. Spinous fin rays usually absent. Pelvic fins jugular or thoracic, with six or fewer rays ; pelvic bones in direct contact with pectoral arch. Caudal region relatively long, with homocercal fin.

Family 1. **Pleuronectidae.** Flat-fishes.

Disc-shaped fishes, much laterally compressed and asymmetrical, resting on one side. Dorsal and anal fins extending almost the whole length of the trunk. Pelvic fins jugular, in front of the pectorals. Scales, when present, minute and ctenoid ; upper side of body coloured, lower side colourless. Eocene to Recent.

The flat-fishes are very numerous in the existing fauna, living on sandy coasts, and some of them entering the mouths of rivers. They are rare among fossils.

Eobothus Eastman. As *Rhombus* Cuv. (=*Bothus* Rafin.), but with fewer

vertebrae. One small species, *E. minimus* Ag. sp., in the Upper Eocene of Monte Bolca. Perhaps also in Oligocene of Roumania.

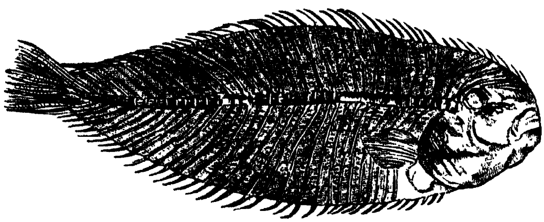


FIG. 255.

Solea kirchbergana H. v. Meyer. Lower Miocene ; Unterkirchberg, near Ulm. Nat. size.

Solea Cuv. is known from the Eocene of Egypt (*S. eocenica* A. S. Woodw.) and the Lower Miocene of Würtemberg (Fig. 255) and Fribourg, Switzerland (*S. helvetica* Leriche). Also from the Miocene of Oran, Algeria, and Gabbro, Leghorn.

Numerous otoliths have been described from Tertiary formations.

Microchirus Bonap. Miocene ; Licata, Sicily ; Gabbro, Leghorn ; and Oran, Algeria.

Achirus Lacép. Miocene ; Oran, Algeria. Recent.

Citharichthys Bleeker. Miocene ; Oran, Algeria. Recent.

Otoliths probably of other genera from Eocene onwards.

Order 9. ACANTHOPTERYGII.

Parietal bones separated by supraoccipital ; squamosal rudimentary and fused with the large pterotic ; premaxilla excluding maxilla from upper border of mouth. No precoracoid arch. Pectoral fin with not more than four or five basals ; pelvic fins far forwards, the pelvic bones in contact with pectoral arch. Some of the rays of the pelvic and median fins spinous, not articulated.

In the existing fauna the *Acanthopterygii* form by far the most numerous group of fishes.

Tribe 1. BERYCIFORMES.

Pelvic fins thoracic, usually with more than five articulated rays in addition to the spine.

Family 1. Berycidae.

Trunk short, compressed, and rather deep, with ctenoid or cycloid scales, rarely naked. Head bones ridged to form large mucus-cavities ; orbits large and lateral ; mouth usually oblique, the jaws, and generally also the palate, with small pointed teeth. Operculum more or less serrated or ridged. Vertebrae 24. Upper Cretaceous to Recent.

The living *Berycidae* are marine fishes, most of them inhabiting considerable depths.

Hoplopteryx Ag. (Fig. 256). Head short. Dorsal fin deep, with a few spaced stout spines in front ; anal fin with four or five spines. Scales large and ctenoid. Common in the Upper Cretaceous, and surviving in the seas off South Australia and New Zealand. *H. zippei* Ag. sp., from the Chalk Marl (Pläner) of Bohemia, *H. lewesiensis* Mant. sp., from the English Chalk, and other species originally referred to *Beryx*.

Sphenocephalus Ag. Upper Cretaceous ; Westphalia. *Pycnosterinx* Heckel

(*Imogaster* Costa) and *Dinopteryx* A. S. Woodw. Upper Cretaceous; Mount Lebanon.

Acrogaster Ag. (*Acanthophoria* Kramberger). Upper Cretaceous; Westphalia and Mount Lebanon.

Homonotus Dixon; *Trachyichthyoides* A. S. Woodw.; *Caproberyx* Regan. English Chalk.

Kansius Hussakof.[1] Upper Cretaceous (Niobrara Group); Kansas.

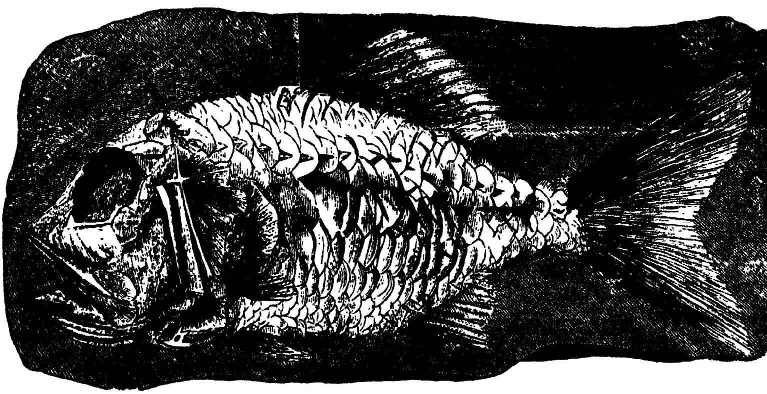


Fig. 256.
Hoplopteryx zippei Agassiz sp. Upper Cretaceous (Lower Pläner); Wehlowitz, Bohemia. $^1/_3$ nat. size (after Fritsch).

Microcentrum Arambourg. *M. melitense* A. S. Woodw. sp.[2] Miocene; Malta, and Oran, Algeria.

The two surviving genera, *Holocentrum* and *Myripristis* Cuv., are represented by extinct species in the Upper Eocene of Monte Bolca.

? *Holocentroidse* Pauca. Oligocene; Roumania.

Family 2. **Polymixiidae.**

As Berycidae, *but with more numerous vertebrae* (28-34) *and last two centra upturned in tail.* Upper Cretaceous to Recent.

Platycormus W. von der Marck. Deep bodied with 14 abdominal, 20 caudal vertebrae. Dorsal and anal fins extended, acuminate in front, with anterior spines pressed together. Scales ctenoid, extending over head and base of median fins. *P. germanus* Ag. sp., from Upper Cretaceous, Westphalia.

Omosoma Costa. Upper Cretaceous; Mount Lebanon.

Berycopsis Dixon. Scales rugose, scarcely ctenoid. *B. elegans* Dixon, English Chalk.

Family 3. **Zeidae.**

Anal fin spines separate from the fin. Oligocene to Recent.

Species from the Upper Oligocene of Steiermark and the Miocene of Oran, Algeria, have been referred to the existing genus *Zeus* Linn. *Cyttoides*

[1] *Hussakof, L.*, Amer. Mus. Novit., no. 357, 1929.

[2] *Bassani, F.*, Atti R. Accad. Sci. Napoli [2], vol. xv., no. 1, 1911.—*Arambourg, C.*, Les Poissons fossiles d'Oran, 1927.

Wettstein, from the Oligocene of Canton Glarus, seems to be related to *Cyttus* Günther. *Proantigonia* Kramberger (*Metoponichthys* Kramb.), from the Upper Miocene, Croatia, may be identical with *Capros* Lacép., which is recorded from the Oligocene of Flörsheim, Mainz, and the Miocene of Oran, Algeria, and Gabbro, Leghorn.

Family 4. **Aphredoderidae.**

Premaxillae not protractile. Vent far forwards. No distinct lateral line. Vertebrae 30. Eocene to Recent.

American freshwater fishes.

Amphiplaga, Asineops, Erismatopterus Cope. Eocene (Green River Shales); Wyoming, U.S.A.

Trichophanes Cope. Oligocene; Colorado and Nevada, U.S.A.

Tribe 2. **PERCIFORMES.**

Pelvic fins thoracic, with not more than five articulated rays in addition to the spine. Mouth usually protractile.

Family 1. **Percidae.** Perches.

Trunk elongated, with ctenoid scales. Premaxilla, mandible, vomer, and palatine with pointed teeth; six or seven branchiostegal rays. One or two dorsal fins, the foremost part with long spines. Cretaceous to Recent.

The perches are predaceous fishes of the tropical and temperate seas and freshwaters. Numerous fossil representatives occur in the Tertiary formations of Europe and North America. Some belong to extinct genera, such as *Paraperca* Sauvage, *Properca* Sauvage, *Smerdis* Ag. (Fig. 257), *Acanus* Ag., *Cyclopoma* Ag., *Platylates* Storms, *Cristigerina* Leriche, and *Mioplosus* Cope. Others have been referred to the existing genera *Perca, Serranus, Pelates, Dules, Gerres, Niphon, Labrax, Lates* Cuv., *Apogon* Lacép., and *Percichthys* Girard.

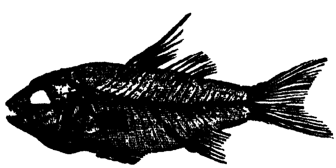


FIG. 257.
Smerdis minutus Ag. Oligocene; Aix-en-Provence. Nat. size.

Centrarchites Cockerell. Scales from Eocene of Walden, Colorado, U.S.A.

Prolates Priem (*Pseudolates* Priem *nec* Macleay). *P. heberti* Gerv. sp. Upper Cretaceous (Montian); Marne, France.

Eoserranus A. S. Woodw. Lameta Beds; Central Provinces, India.

Family 2. **Carangidae.** Horse-mackerels.

Trunk laterally compressed, deep or elongated, naked or with small scales. Teeth conical. Spinous portion of the dorsal fin feeble and shorter than the soft portion; pelvic fins sometimes rudimentary or absent; caudal pedicle constricted. Cretaceous or Eocene to Recent.

Marine predaceous fishes of the tropical and temperate zones, common in Tertiary formations.

Aipichthys Steindachner. Trunk deep and laterally compressed; extended

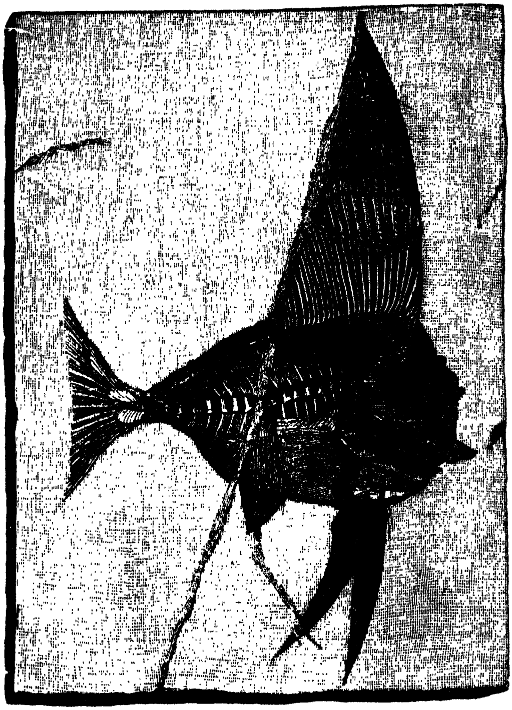


FIG. 258.
Semiophorus velifer Ag. Upper Eocene ; Monte Bolca. $^1/_2$ nat. size (after Agassiz).

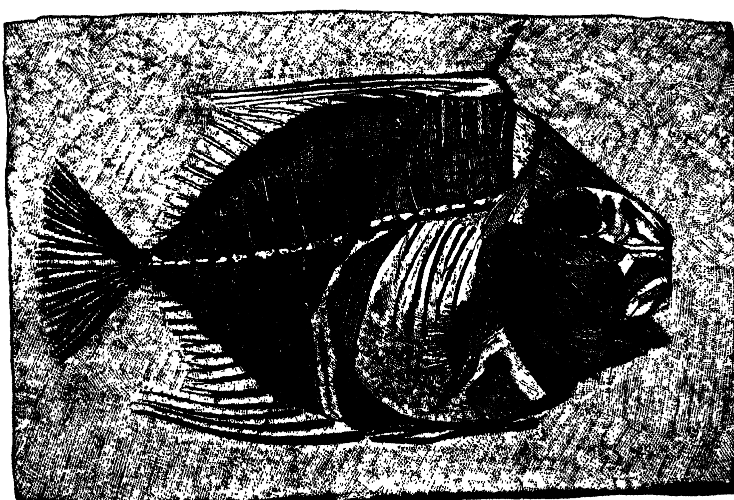


FIG. 259.
Acanthonemus filamentosus Ag. Upper Eocene ; Monte Bolca. $^2/_3$ nat. size (after Agassiz).

dorsal fin deep and pointed in front; anal less extended; caudal forked. Thickened ventral ridge scales. *A. pretiosus* Steind. Cretaceous; Istria and Dalmatia. Other species in Upper Cretaceous, Mount Lebanon and England.

Bathysoma Davis. Upper Chalk; S. Sweden.

Platax Cuv. Fossil in the Upper Eocene of Monte Bolca and in the Crag (Lower Pliocene) of Norfolk. Recent.

Zanclus Commers. Eocene and Recent.

Semiophorus Ag. (Fig. 258); *Acanthonemus* Ag. (Fig. 259); *Amphistium* Ag.; *Carangopsis* Ag. Upper Eocene; Monte Bolca.

Archaeus Ag. (*Archaeoides* vom Rath). Oligocene; Canton Glarus.

Other genera with extinct representatives are the following:—*Vomer* Cuv., *Caranx* Cuv., *Lichia* Cuv., *Trachinotus* Lacép., *Seriola*, *Equula* Cuv., etc.

Lampris Retzius, of an allied family, occurs in the Miocene diatomaceous earth of Santa Barbara Co., California.

Family 3. **Menidae.**[1]

Trunk laterally compressed. Teeth small and conical or wanting. Dorsal fin extended, without spines. Eocene to Recent.

Mene Lacép. (*Gasteronemus* Ag.). Extinct species in the Upper Eocene of Monte Bolca, the Phosphates of Gafsa, Tunis, and the Tertiary of Antigua.

Family 4. **Teuthididae.**

As Percidae, *but with only marginal cutting teeth and the anal spines stout and numerous.* Oligocene to Recent.

Archaeoteuthis Wettstein. Oligocene; Canton Glarus.

Family 5. **Sparidae.** Sea-breams.

Brightly coloured, rather deep-bodied fishes, with very delicately serrated ctenoid scales. Margin of jaws provided in front with conical or cutting teeth of different shapes, which are usually followed behind by several rows of round or oval grinding teeth; palatine and vomer toothless. Dorsal fin single, the anterior spinous part almost similar to the posterior soft part; anal fin with three spines. Eocene to Recent.

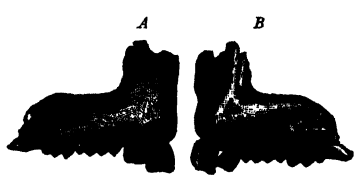


FIG. 260.
Premaxillae of *Sargus*, outer (*A*) and inner (*B*) views. Recent; Mediterranean. Nat. size.

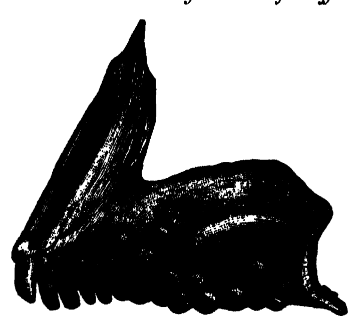


FIG. 261.
Right premaxilla of *Chrysophrys aurata* Linn. Inner aspect. Recent; Mediterranean. Nat. size.

[1] *Astre, G.*, Le Carangidé des phosphates tunisiens. Bull. Soc. Hist. Nat. Toulouse, vol. lvi., p. 501, 1927.—*Cramer, R.*, *Mene rhombeus* (Volta sp.). Zeitschr. Deutsch. Geol. Ges., vol. lviii., p. 181, 1906.

The sea-breams, which are easily recognised by their peculiar dentition, live at the present day in the tropical seas, feeding especially on Mollusca and Crustacea, which they crush with their teeth.

Sparnodus Ag. occurs in the Upper Eocene of Monte Bolca. *Sargus* Cuv. (Fig. 260), and *Chrysophrys* Cuv. (Fig. 261), range from the Miocene to existing seas.

Paracalamus Arambourg. Miocene; Oran, Algeria.

Lutianus Bloch. *L. avus* W. K. Gregory.[1] Lower Oligocene; Florida, U.S.A. Recent.

Dentex Cuv. Upper Eocene; Monte Bolca and Belgium.

Ctenodentex Storms. Upper Eocene; Belgium. Middle Eocene; Egypt.

Family 6. **Sciaenidae.**

Percoids with great development of slime-pits on head. Teeth conical or villiform, restricted to margin of jaws. Spinous portion of dorsal fin much less extended than soft portion; anal fin short-based with one or two spines. Oligocene to Recent.

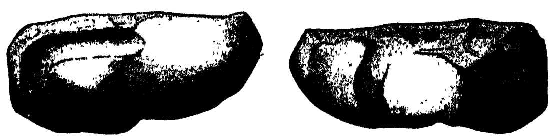


FIG. 262.

Otolithus (Sciaena) holsaticus Koken. Otolith, inner and outer views, $1^1/_2$ times nat. size. Miocene; Holstein (after Koken).

Sciaena Cuv. (Fig. 262). Otoliths from Oligocene and Miocene of Germany and Southern United States.

Pogonias Lacép. *P. multidentatus* Cope,[2] an upper pharyngeal from Miocene, Virginia, U.S.A.

Diaphyodus Schafhäutl. Pharyngeal plates trapezoidal, with mosaic of polygonal teeth. European Eocene.

Many otoliths of existing genera from Oligocene and later Tertiaries.

Family 7. **Pomacentridae.**

Short, laterally compressed, spiny-finned fishes, with ctenoid scales. Single nostril on each side. Dentition feeble. Palatines toothless. Lower pharyngeal bones fused. Dorsal fin extended, with numerous spines; anal fin with two or three spines. Eocene to Recent.

Odonteus Ag. Upper Eocene; Monte Bolca.

Family 8. **Labridae.** Wrasses.

Brilliantly coloured fishes with cycloid scales and thick fleshy lips. Teeth on margin of jaws powerful; palate toothless. United lower pharyngeals much thickened and forming a plate beset with rounded, rarely acuminate grinding teeth; upper pharyngeals usually separate, bearing similar teeth. Eocene to Recent.

The wrasses chiefly inhabit tropical seas at the present day.

Phyllodus Ag. (Fig. 263). Known only by pharyngeals bearing smooth, thin, flattened grinding teeth. Grinding surface of upper plate slightly

[1] Florida State Geol. Surv., Bull. no. 5, p. 7, 1930.
[2] *Smith, B.*, Amer. Journ. Sci., vol. xxviii., p. 275, 1909.

concave, lower convex. Teeth arranged in rows, the middle row large. Several layers of successional teeth usually lie beneath those in function. Eocene and Miocene; Europe and North America.

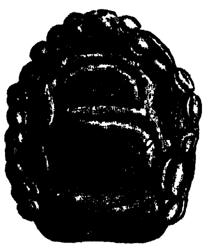


FIG. 263.

Phyllodus medius Ag. Lower pharyngeal dentition, nat. size. London Clay: Sheppey (after Cocchi).

Egertonia Cocchi. As *Phyllodus*, but pharyngeal teeth nearly uniform. Lower Eocene; London and Paris Basin. *Egertonia stromeri* Weiler. U. Eocene; Egypt.

Labrodon Gervais (*Nummopalatus* Rouault; *Pharyngodopilus* Cocchi) (Fig. 264). Lower pharyngeal triangular, covered with a pavement of numerous small, round or oblong grinding teeth, of which there are always several superimposed layers. Upper pharyngeals separate, triangular, covered with grinding teeth. Eocene; Virginia. Eocene to Pliocene; Europe.

Taurinichthys Cocchi. Miocene; Italy.

Pseudovomer Sauvage. Miocene; Licata, Sicily.

Gillidia Eastman. *G. antiquus* (*Toxotes antiquus*) Ag. sp. Upper Eocene; Monte Bolca.

Eolabroides Eastman. For "*Crenilabrus*" *szajnochae* de Zigno. Upper Eocene; Monte Bolca.

The existing genera *Labrus* Linn,[1] *Julis*, *Crenilabrus* Cuv., and *Scarus* Forsk.,[2] are also represented in the Tertiaries. Numerous otoliths.

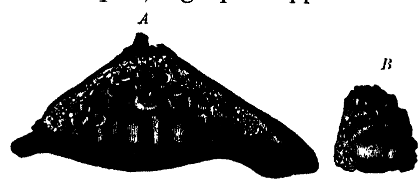


FIG. 264.

Labrodon multidens Münst. sp. Miocene; Neudörfl a. d. March. *A*, lower pharyngeal with dentition. *B*, an upper pharyngeal. Nat. size.

Platylaemus Dixon;[3] *Pseudosphaerodon* Noetling. Middle Eocene; S. England, Belgium, N. Germany, Egypt, S. Nigeria.

Family 9. **Chromidae.** (*Cichlidae*).

Tropical and subtropical freshwater fishes much resembling Labridae, *but scales usually ctenoid and only a single nostril on each side.* Eocene to Recent.

Priscacara Cope.[4] Eocene Green River Shales; Wyoming, U.S.A.

Chromis Cuv. Miocene; Oran, Algeria.

Cichlasoma Swainson.[5] *C. woodringi* Cockerell. Miocene; Las Cahobas, Haiti.

Tribe 3. SCOMBRIFORMES.

Differing from Perciformes *in the maxillae being fixed to the non-protractile premaxillae and forming a pointed beak. Caudal pedicle contracted and caudal fin rays deeply overlapping the hypural bone.*

[1] *Brunati, R.*, Sopra alcune ossa faringee fossili spettanti al genere *Labrus*. Atti Soc. Ital. Sci. Nat., vol. xlviii., p. 103, 1909.

[2] *Peyer, B.*, *Scarus baltringensis* Probst. Eclogae geol. Helvet., vol. xxi., p. 413, 1928.

[3] *Weiler, W.*, Abhandl. Bay. Akad. Wiss., math.-naturw. Abt., n.s., vol. i., p. 14, 1929.

[4] *Haseman, J. D.*, Bull. Amer. Mus. Nat. Hist., vol. xxxi., art. 8, 1912.

[5] *Myers, G. S.*, Copeia, no. 167, p. 33, 1928.

Family 1. **Scombridae.** Mackerels.

Trunk elongate-fusiform, naked or with small scales. Teeth conical. Pelvic fins thoracic; two dorsal fins, the hinder usually consisting of separate tufts. Eocene to Recent.

Eococlopoma, Eothynnus, Scombrinus A. S. Woodw. Skulls from Lower Eocene (London Clay), Sheppey.

Scombramphodon A. S. Woodw. (*Amphodon* Storms *nec* Peters). Oligocene (Rupelian); Belgium. Lower Eocene (London Clay) and Middle Eocene; England.

Sphyraenodus Ag. (*Dictyodus* Owen; *Pelamycybium* Toula). *S. priscus* Ag. London Clay; Sheppey. *S. rupeliensis* Dollo and Storms sp. Rupelian; Belgium. Miocene; Vienna.

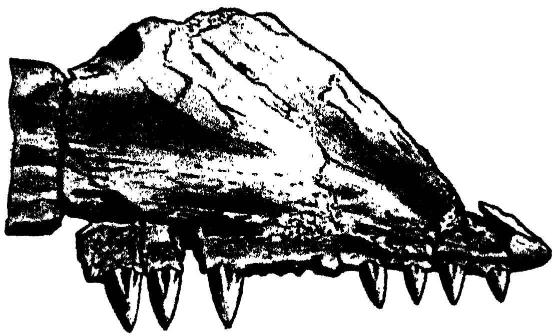


Fig. 265.
Cybium dumonti Van Bened. sp. Premaxilla. Oligocene; Steendorp. 1/2 nat. size (after Leriche).

Cybium Cuv. (*Scomberodon* P. J. Van Beneden) (Fig. 265). Eocene, Oligocene, and Miocene of Europe. *Neocybium* Leriche. Teeth smaller than in *Cybium*, and vertebral centrum with three lateral pits. Oligocene (Rupelian); Belgium.

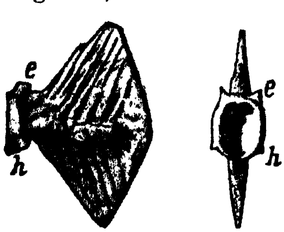


Fig. 266.
Pelamys sp. Hypural, with upper (*e*) and lower (*h*) processes. Oligocene; Waldböckelheim.

Stereodus Owen. Miocene; Malta.

Scomber Linn. *S. dolloi* Leriche, a skull from Middle Eocene, Brussels. Oligocene and Miocene species from Croatia and Oran, Algeria. *Auxis* Cuv., also Miocene, perhaps Eocene.

Thynnus Cuv. (*Orcynus* Cuv.). Upper Eocene; Monte Bolca. European Oligocene and Miocene. Miocene; Oran, Algeria. Pliocene Crags of Belgium and England.

Pelamys Cuv. (Fig. 266). Eocene to Recent.

Ardiodus White. Teeth from Lower Eocene, Kent.

Palimphyes Ag.; *Isurichthys* A. S. Woodw.; *Opisthomyzon* Cope (allied to *Echeneis* Art.). Oligocene; Canton Glarus. *Isurichthys* also in Tertiary, Shushter, Persia.

Megalolepis Kramb., and a genus allied to *Echeneis* (*E. carpathica* Szajnocha), in the Lower Menilite shales of Galicia.

Family 2. **Trichiuridae.**

Elongated and laterally compressed, almost ribbon-shaped fishes. Gape of mouth wide, jaws and palatine bones with powerful conical teeth. Dorsal and anal fins much extended, with unarticulated rays; pelvic fins sometimes rudimentary or wanting. Eocene to Recent.

The *Trichiuridae* are predaceous fishes of the tropical and sub-tropical seas, living both near the coasts and also in deep water.

Thyrsitocephalus G. vom Rath. Paired fins small; finlets behind dorsal and anal fins. *T. alpinus* G. vom Rath. Oligocene; Canton Glarus.

Trichiurides Winkler. Barbed teeth from the Eocene and Oligocene of Belgium and Alsace, from the Miocene of Bordeaux, Vienna, and Sardinia.

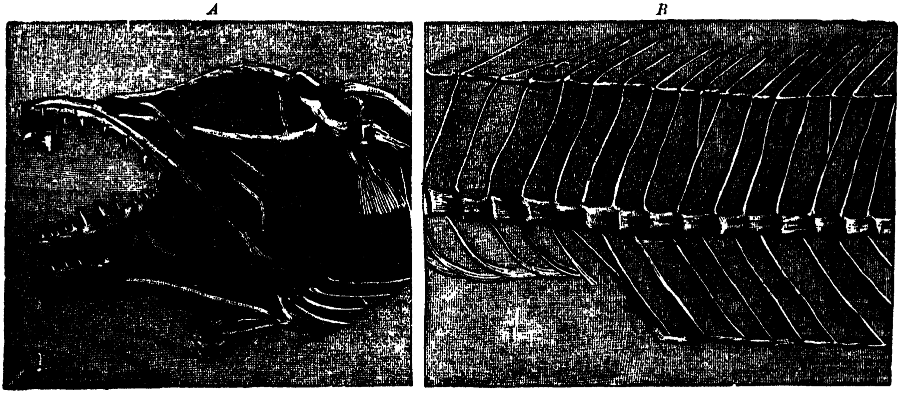


Fig. 267.
Lepidopus (*Anenchelum*) *glarisianus* Blainv. Oligocene; Matt, near Glarus.
A, head. *B*, portion of trunk. Nat. size (after Wettstein).

Similar teeth (*Trichiurus oshosunensis* White) from Eocene, S. Nigeria. Some probably referable to *Lophiidae*.

Hemithyrsites Sauvage. Miocene; Licata, Sicily. ? *Gempylidae*.

Extinct species of the existing *Lepidopus* Gouan (*Anenchelum* Blv.; *Lepidopides* Heckel) are found in the Oligocene black slates of Glarus (Fig. 267), in the Menilite shales of the Carpathians (*L. carpathicus* Kramb.), and in the Miocene of Sicily, Tuscany, and Algeria.

Family 3. **Palaeorhynchidae.**

Elongated, low, and laterally compressed fishes. Snout produced into a long beak; jaws toothless or with very small denticles. Vertebrae long and slender; spinous processes and ribs delicate. Pelvic fins thoracic, with several rays; dorsal fin extending from the occiput to the tail; anal fin extending from the anus nearly to the cleft caudal fin. Eocene to Miocene.

Palaeorhynchus Blainville (Fig. 268). Jaws of equal length; nearly fifty dorsal fin spines, as numerous as the vertebrae below them; about fifteen to eighteen short divided rays in hinder part of dorsal fin. *P. glarisianus* Blv. Oligocene; Canton Glarus. *P. zitteli* Kramb. sp. Upper Eocene; Galicia. Other species in Oligocene of Croatia, Bavaria, and Alsace; also in Lower Miocene, Chiavon, Vicentin.

Hemirhynchus Ag. (*Homorhynchus* P. J. Van Beneden). Mandible much shorter than rostrum; dorsal fin spines much more numerous than the vertebrae beneath them. *H. deshayesi* Ag. Middle Eocene (Calcaire Grossier); Paris. *H. colei* Ag. sp. Oligocene; Canton Glarus. *H. bruxelliensis* Van Ben. Middle Eocene; Brussels.

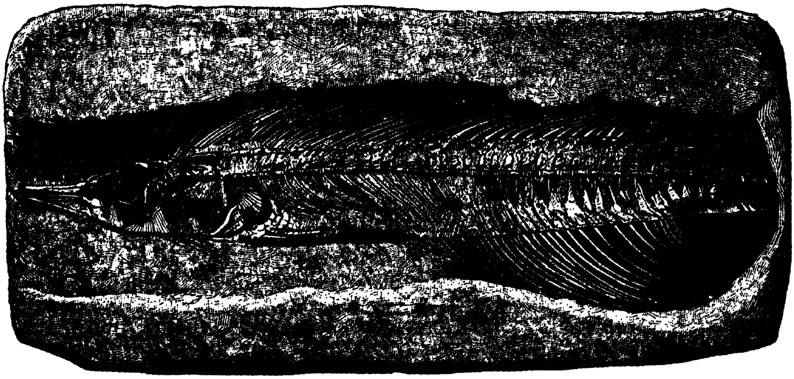


FIG. 268.
Palaeorhynchus zitteli Kramb. sp. , Upper Eocene ; Rajcza, Galicia. 1/3 nat. size.

Family 4. **Blochiidae.**

Elongated fishes with very long cylindrical rostrum projecting beyond the large mouth. The entire trunk covered with cordiform or rhombic bony scales, which are

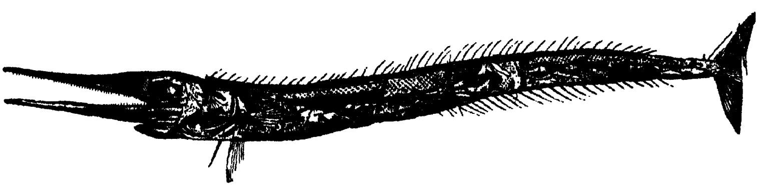


FIG. 269.
Blochius longirostris Volta (with incomplete rostrum). Upper Eocene ; Monte Bolca. 1/6 nat. size (after Agassiz).

mostly keeled and overlap each other. Dorsal fin arising at the occiput and extending almost to the caudal fin, composed of a spaced series of flexible spines ; anal fin also much extended and consisting of similar spines ; caudal fin large. Upper Cretaceous to Oligocene.

Blochius Volta (Fig. 269), known by nearly complete fishes from the Upper Eocene of Monte Bolca. Two longitudinal series of scales somewhat enlarged on each flank.

Cylindracanthus Leidy (*Coelorhynchus* Ag. *nec* Giorna; *Glyptorhynchus* Leriche)[1] (Fig. 270). A cylindrical or somewhat depressed elongated rostrum like that of *Blochius*, consisting entirely of dermal tissue (cosmine) and longitudinally ribbed, each rib being the outer edge of a separate sector ; the central cavity simple distally but divided by a median septum proximally. *C. rectus* Ag. Eocene ; England, Belgium, Italy, and Nigeria. Other species in the Eocene of Bavaria, Spain, Egypt, India, and Alabama. *C. denticulatus* Leriche.

[1] *Carter, J. T.*, Geol. Surv. Nigeria, Occasional Paper No. 5, 1927.—*Leriche, M.*, Ann. Soc. Roy. Zool. Belg., vol. lvi., p. 121, 1926.

Apparently associated with vertebrae in the Oligocene of Belgium. Smaller species also in the Upper Cretaceous of England, Belgium, and Mount Lebanon.

Family 5. **Xiphiidae.** Sword-fishes.

Elongate-fusiform fishes with a long pointed rostrum formed by the united premaxillae and nasals. Teeth small or absent. Forked caudal fin powerful, the rays very deeply overlapping the large hypural. Eocene to Recent.

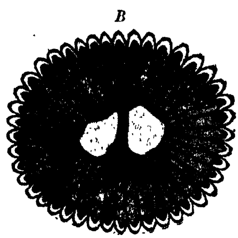


FIG. 270.

Cylindracanthus sp. Rostrum in side view (*A*) nat. size, and in transverse section (*B*) enlarged. Eocene; Kressenberg, Bavaria.

Xiphiorhynchus P. J. Van Beneden. Rounded rostra from Lower Eocene (London Clay), Sheppey; Middle Eocene, Brussels; Upper Eocene, Egypt; and Miocene, Algeria.

Brachyrhynchus P. J. Van Beneden. Middle Eocene; Belgium. Miocene and Pliocene; Belgium, France, and Italy.

Acestrus A. S. Woodw. Skull with frontals marked by smooth radiating ridges. London Clay; Sheppey.

Xiphias Art.; *Histiophorus* Lacép. Eocene to Recent; Europe and North America. Numerous remains of *Xiphias rupeliensis* Leriche, in Oligocene (Rupelian) of Belgium.

Tribe 4. GOBIIFORMES.

Head depressed, mouth protractile. Pectoral fins with extended base on flank; spinous dorsal, if present, of few flexible spines. No bony suborbital stay for preoperculum.

Family 1. **Gobiidae.** Gobies.

Elongated fishes with stout caudal pedicle. Pelvic fins often united into a disk; posterior dorsal and anal fins equal and opposite, more extended than spinous dorsal. Oligocene or Miocene to Recent.

Gobiopsis Priem, from the Eocene of Aftab, Persia, is very doubtfully placed here; also the so-called *Gobius microcephalus* Ag., from Upper Eocene, Monte Bolca.

Gobius Linn. Imperfect specimens from Lower Oligocene, Galicia. Otoliths from Miocene.

Callionymus Linn. *C. macrocephalus* Kramb. Upper Miocene; Croatia.

Family 2. **Trachinidae.**

As Gobiidae, *but gill opening wide and pelvic fins never united.* Eocene or Oligocene to Recent.

Callipteryx Ag. Upper Eocene; Monte Bolca.

Trachinus Linn. *T. dracunculus* Heckel. Upper Miocene; Croatia. Numerous otoliths of other species.

Tribe 5. BLENNIIFORMES.

Pectoral fins with extended base on flank; pelvic fins jugular, reduced or absent; dorsal fin spines numerous but usually flexible. No bony suborbital stay for preoperculum.

Family 1. **Blenniidae.**

Elongated fishes with stout caudal pedicle. Dorsal fin occupying most of back, often subdivided; anal also extended. Eocene to Recent.

Pterygocephalus Ag. Supposed allied to existing *Cristiceps* Cuv. Upper Eocene; Monte Bolca.

Fossils from the Upper Miocene have been referred to the existing *Blennius* Linn. and *Clinus* Cuv.

? *Problennius* Priem. Eocene; Aftab, Persia.

Tribe 6. LOPHIIFORMES. (Pediculati.)

Broad pectoral fins supported by elongated basals; pelvic fins jugular or absent; anterior dorsal fin reduced to a few isolated tentacle-like spines; soft dorsal and anal short.

Family 1. **Lophiidae.** Angler Fishes.

Head very large, wide and depressed; mouth horizontal. Body contracted, conical and tapering. Eocene to Recent.

Lophius Linn. *L. brachysomus* Ag. Upper Eocene; Monte Bolca. *L. dolloi* Leriche. Oligocene (Rupelian); Belgium — jaws only. Also Miocene; Oran, Algeria.

Family 2. **Antennariidae.**

Head and body more or less laterally compressed; mouth vertical or very oblique. Pectoral fins forming elbow-like angle. Eocene to Recent.

Histionotophorus Eastman (*Histiocephalus* de Zigno *nec* Diesing). *H. bassanii* de Zigno, a fish 6 cm. in length from Upper Eocene, Monte Bolca.

Tribe 7. SCORPAENIFORMES. (Scleroparei.)

Pectoral fins with extended base on flank; pelvic fins thoracic. One bone of circumorbital ring produced into stay for preoperculum, which is spiny.

Family 1. **Scorpaenidae.**

Head armed with spines. Post-temporal bone free from cranium. Dorsal fin with 8 *to* 16, *anal with* 3 *spines.* Eocene to Recent.

Ampheristus König. Skull from London Clay, Sheppey.

Scorpaenoides Priem. Eocene; Roumania.

Ctenopoma Heckel; *Scorpaenopterus* Steindachner. Miocene; Vienna.

The existing *Scorpaena* Linn. seems to be represented in the Miocene of Croatia and Algeria.

Family 2. **Cottidae.**

Head usually broad and depressed, with narrow interorbital region. Post-temporal bone free. Anal fin without spines. Eocene to Recent.

Eocottus A. S. Woodw. With small scales. Upper Eocene; Monte Bolca.

Lepidocottus Sauvage (Fig. 271). With ctenoid scales. Freshwater Oligocene; Aix-en-Provence, France; Monte Viale, near Vicenza. Miocene; Oeningen, Baden; Ulm, Würtemberg; Chiavon, Vicentin.

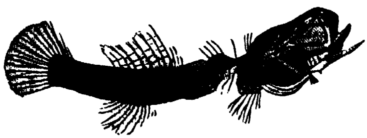


FIG. 271.
Lepidocottus brevis Ag. sp. Miocene; Oeningen, Baden. Nat. size (after Agassiz).

Cottus Linn.[1] The existing *C. uncinatus* Reinhardt in nodules in Pleistocene clay, Green's Creek, Ottawa, Canada. Fragments in Pleistocene of Upland, Sweden, and in freshwater deposits in Idaho, Nevada, and Oregon, U.S.A. *C. cervicornis* Storms. Oligocene (Rupelian); Belgium.

? *Cottopsis* Priem. Eocene; Aftab, Persia.

Family 3. **Triglidae.** Gurnards.

Suborbitals enlarged and covering cheek; post-temporal bone fused with cranial roof, and supracleithrum displaced backwards to allow articulation with cleithrum. Spinous dorsal less extended than soft dorsal; anal without spines. Oligocene to Recent.

Trigla Linn. To this existing genus are referred ornamented plates from the Oligocene (Rupelian), Belgium, and imperfect fishes from the Oligocene of Mainz and the Miocene of Vienna, Italy, Sicily, and Algeria.

Numerous otoliths.

Tribe 8. CHAETODONTIFORMES.

Perciform fishes with very short brain case, long face, and small terminal mouth. Trunk deepened and dorsal fin spines well developed.

Family 1. **Chaetodontidae.**

Maxilla separate from premaxilla. Scales small or minute, ctenoid, densely covering soft portions of median fins. Eocene to Recent.

Pygaeus, Pomacanthus Ag.; *Parapygaeus* Pellegrini. Upper Eocene; Monte Bolca. Species of existing genera *Ephippus* Cuv. and *Scatophagus* Cuv., also at Monte Bolca. Species of *Holacanthus* Lacép. in Middle Eocene, France, and Lower Miocene, Chiavon, Vicentin.

Chelmo Cuv. *C. fossilis* de Beaufort. Miocene; South Celebes. Recent, on coral reefs.

[1] *Jordan, D. S.*, Fossil Sculpin from Nevada regarded as *Cottus beldingi*. Proc. U.S. Nat. Mus., vol. lxv., art. 6, 1924.—*Leriche, M.*, Les *Cottus* fossiles. C.R. Assoc. Franç. Adv. Sci., 1904, p. 677.

Family 2. **Acronuridae.**

Maxilla fused with premaxilla. Jaws with a row of cutting teeth. Scales minute, ctenoid. The tail in adult examples provided with one or several bony plates or spines. Eocene to Recent.

The living genera dwell chiefly in the vicinity of coral reefs.

The existing genera *Acanthurus* Forsk. and *Naseus* Commerson are recorded from the Upper Eocene of Monte Bolca; the former also from the Calcaire Grossier of Paris and the Miocene of Vienna. An extinct species of *Zebrasoma* Swainson is known from the Tertiary of Antigua, West Indies.[1]

Aulorhamphus de Zigno (*Calamostoma* Steind. *nec* Ag.) (Fig. 272). Upper Eocene; Monte Bolca.

Apostasis Kramberger. Oligocene; Steiermark and Switzerland. Miocene; Croatia and Tuscany.

Tribe 9. **PLECTOGNATHI.**

Skin covered with roughened scales, bony spines or plates, rarely naked. Skeleton incompletely ossified. Maxillae and premaxillae fused together into a solid beak. Gills pectinate. Pelvic fins wanting or represented by spines; dorsal fin with articulated rays opposed to the anal fin.

Family 1. **Gymnodontidae.**

Trunk short and deep, naked or covered with bony spines. Jaws beak-shaped, with a cutting dental plate above and below, either undivided or in right and left halves, and with small crushing plates (sometimes rudimentary) within. No dorsal spines. Eocene to Recent.

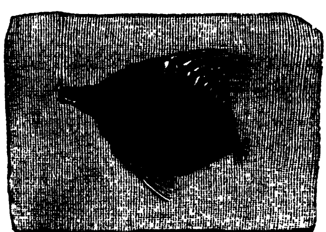


FIG. 272.
Aulorhamphus canossae Heckel sp. Upper Eocene; Monte Bolca. Nat. size.

FIG. 273.
Diodon (*Progymnodon*) *hilgendorfi* Dames. Upper (*A*) and lower (*B*) jaws. Eocene; Egypt. Nat. size.

Tetrodon Linn. Jaws from the Miocene of Sardinia and Pliocene of Italy. ? *T. pygmaeus* de Zigno. Upper Eocene; Monte Bolca.

Triodon Cuv. Jaws of *Triodon antiquus* Leriche. Middle Eocene; Brussels. *T. cabindensis* Leriche. Lower Eocene; Congo Free State.

Diodon Linn.[2] (*Megalurites* Costa; *Enneodon* Heckel; *Heptadiodon* Bronn; *Gymnodus* Delfortrie; *Progymnodon* Dames) (Fig. 273). Small fishes 10 cm. in length, *D. erinaceus* Ag., from Upper Eocene, Monte Bolca. Jaws of *D.*

[1] *Hussakof, L.*, Bull. Amer. Mus. Nat. Hist., vol. xxiii., art. iii., 1907.
[2] *Pasquale, M.*, Avanzi di *Diodon vetus*. Rendic. R. Accad. Sci. Napoli [11], vol. iii., p. 71, 1905 (with Bibliography).

scillae Ag. from Miocene of Italy, Sicily, and Malta. Other jaws from Eocene, Italy, Egypt (Fig. 273), and India; Oligocene, Italy; Miocene, Italy, Sicily, and Oran, Algeria (? *Chilomycterus* Bibron), and France; Tertiary Phosphate Beds, South Carolina, U.S.A.

Orthagoriscus Bloch and Schneider. Large jaws of *O. pileatus* P. J. van Beneden, Miocene or Pliocene, Antwerp. Wrongly recorded from English Chalk.

Family 2. **Trigonodontidae.**

Jaws with cutting dental plates but no crushing plates within. Upper Cretaceous to Pliocene.

Stephanodus Zittel. Cutting dental plate clearly showing its component teeth. *S. splendens* Zitt. Upper Cretaceous; Sahara, Egypt, and Arabian Desert.

FIG. 274.
Eotrigonodon serratus Gervais sp. Tooth, outer (*a*) and inner (*b*) view. Eocene; Chaumont, Oise. Nat. size (after Priem).

Eotrigonodon Weiler (Fig. 274). Cutting dental plate serrated or pectinated. *E. serratus* Gervais sp. (Fig. 274). Eocene; N. France and Belgium. Var. *aegyptiaca* in Middle and Upper Eocene, Egypt.

Trigonodon Sismonda Cutting dental plate with smooth edge. Middle Miocene to Pliocene; Europe, North Africa, and New Zealand.

Family 3. **Sclerodermidae.**

Jaws with a small number of separate teeth. Skin with scales or roughened. Dorsal spines usually present. Eocene to Recent.

The existing genus *Ostracion* and the extinct *Spinacanthus* Ag. (*Protobalistum* Massal.) have representatives in the Upper Eocene of Monte Bolca. *Ostracion* also occurs in the Eocene of Belgium and the Oligocene of Roumania. The extinct genera *Acanthoderma* and *Acanthopleurus* Ag. occur in the Oligocene black slates of Glarus; *Marosia* de Beaufort, in the Miocene of South Celebes. The Eocene and Oligocene teeth described as *Ancistrodon* Roemer (*Grypodon* Hay) (Fig. 275), may belong, at least in part, to the pharyngeal dentition of Scleroderms. Similar Cretaceous teeth belong to Pycnodonts (p. 133).

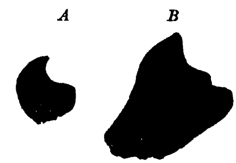


FIG. 275.
Pharyngeal teeth. *A, Ancistrodon libycus* Dames. Upper Chalk; Gasr Dachl, Libyan Desert. *B, Ancistrodon armatus* Gervais sp. Eocene; Mokattam, near Cairo (after Dames).

Balistes Linn. Extinct species in the Miocene of Algeria and South Celebes.

Range and Distribution of Fossil Fishes.[1]

Notwithstanding the apparently favourable circumstances for the preservation of fishes due to their living in water, their geological history is still very

[1] *Woodward, A. S.*, The Study of Fossil Fishes. Proc. Geol. Assoc., vol. xix., p. 266, 1906. —The Use of Fossil Fishes in Stratigraphical Geology. Quart. Journ. Geol. Soc., vol. lxxi., p. lxii, 1915.

imperfectly known. Complete skeletons, it is true, are rather numerous in clayey, calcareous, or marly shales, which were laid down as fine mud on the bottom of former lakes and near the shore in seas. On the other hand, in rocks of coarser grain (sandstone), in very many shore deposits, and also in deep-sea limestones, there are usually only isolated teeth, scales, dermal plates, vertebrae, scattered bones of the skeleton, and otoliths, which are extremely difficult to determine. In many marine, lacustrine, and fluviatile deposits, fish remains are almost completely wanting, so that the formations rich in fossils are usually separated from each other by a series of strata which represent long periods of time.

The oldest undoubted traces of fishes both in Europe and North America occur in rocks of **Ordovician** age. The minute conical teeth found by Rohon among the Conodonts in the Glauconite Sands in the Government of Leningrad, Russia, resemble in structure those of fishes. The dermal plates of *Astraspis* from rocks apparently of the Trenton Series in Colorado, Wyoming, Montana, and South Dakota, U.S.A., seem to belong to primitive Cephalaspidian *Ostracodermi*.

The next known fish remains are from the **Upper Silurian**. They are found in the Ludlow Bone-bed, in the light, fissile, dolomitic limestone of the island of Oesel in the Baltic, and in sandy shales in Bohemia, Podolia and Galicia. They are also found in the Onondaga Group of Pennsylvania. They are still more abundant in the Downtonian formations of England, Scotland, Spitzbergen, and Norway, which form the Passage Beds to the overlying Devonian. The determinable forms are all primitive *Ostracodermi* and *Acanthodii*, which must have been either freshwater or shore-living fishes.

In the **Devonian** era fishes begin to attain a great development, and are sometimes discovered in a remarkable state of preservation, especially in the Old Red Sandstone of Great Britain, the Baltic States, Podolia, and Galicia, and in the corresponding formations of Germany, Spitzbergen, and North America. An especially well-preserved series of *Arthrodira* has been obtained from the Upper Devonian of Wildungen, near Kassel. Scattered fish remains, such as plates of *Ostracodermi* and *Arthrodira* and spines of *Elasmobranchii*, also occur in the Devonian of the Eifel, Nassau, Westphalia, Belgium, N. France, Australia, and Antarctica. Gigantic Arthrodires (*Dinichthys*, *Titanichthys*, *Diplognathus*) and *Elasmobranchii*, especially *Cladoselachidae*, are remarkably abundant in the Middle and Upper Devonian of Ohio, Wisconsin, and New York. The Devonian fish fauna consists of *Ostracodermi*, *Arthrodira*, many Ganoids (*Crossopterygii* and *Chondrostei*), Dipnoans (*Dipteridae*, *Phaneropleuridae*), and Elasmobranchs (*Pleuropterygii*, *Acanthodii*, *Selachii*). Most of the groups which pass upwards from the Silurian become extinct at the end of the Lower Devonian. The fishes of the Old Red Sandstone are freshwater forms, and the *Crossopterygii* make a nearer approach to lung-breathers than any fishes of later periods.

The fishes of the **Carboniferous** System are obtained partly from the marine Carboniferous Limestone, partly from the shales and sandstones of the productive Coal Measures. The *Ostracodermi* and *Arthrodira* have become extinct, and the enormous development of the *Elasmobranchii*,[1] of which, however, only teeth and fin spines are commonly preserved, sharply dis-

[1] *Hay, O. P.*, The Chronological Distribution of the Elasmobranchs. Trans. Amer. Phil. Soc., vol. xx., 1901.

tinguishes the Carboniferous fish fauna from that of the Devonian period. The *Cochliodontidae*, *Psammodontidae*, *Copodontidae*, *Edestidae*, and *Petalodontidae* are most abundant in the Carboniferous Limestone, while the *Hybodontidae* are also well represented; the *Acanthodii* and *Pleuropterygii* continue, the *Pleuracanthidae* begin. The heterocercal Ganoids are the principal associates of the *Elasmobranchii*; the *Crossopterygii* and *Dipnoi* are still present, but in diminished numbers. On the whole, the Carboniferous fauna marks the beginning of the adaptation of fishes for a free-swimming life in the open sea.

The fishes of the **Permian** System are closely similar to those of the productive Coal Measures. They occur in the Rothliegenden of the Saar Basin, Bohemia, Saxony, Silesia, and France; in the Marl Slate and Magnesian Limestone of England; in the Kupferschiefer of Thuringia and Hesse; and in the probably contemporaneous strata of Texas and New Mexico. The *Chondrostei* are by far the most numerous, and in the Upper Permian they are accompanied by a forerunner of the *Protospondyli* (*Acentrophorus*). Of the *Crossopterygii*, *Coelacanthus* and *Megalichthys* alone survive in Europe. Among the *Dipnoi*, the genera *Ctenodus* and *Sagenodus* are especially widely distributed. In comparison with the Carboniferous fish fauna, that of the Permian period is noticeably destitute of *Elasmobranchii*. Here, however, the remarkable *Pleuracanthidae* and *Edestidae* attain their maximum development, and are associated with a few *Cochliodontidae* (*Menaspis*), *Petalodontidae* (*Janassa*), and *Acanthodidae*. The four latter families now become extinct.

The abrupt break in development, which is observable in most sections of the animal and plant world at the close of the Palaeozoic epoch, is also conspicuous among the fishes, although the **Triassic** fish fauna exhibits several resemblances to that of the Permian. Very few specimens are found in the Bunter Sandstone, which is a land deposit forming the base of the Triassic System in Europe, but fossil fishes become numerous in the marine formations of the Muschelkalk and Rhaetic series, and they are especially well preserved in the black shales of Perledo near Lake Como, Besano and Lumezzane in Lombardy, Raibl in Carinthia, Lunz in Lower Austria, and Giffoni near Naples; in the asphalt shales of Seefeld and other localities in the Tyrol; and in the dolomite of the neighbourhood of Salzburg. A few occur in the Keuper Sandstone of Würtemberg and England. Nearly similar fishes are also known from the corresponding formations in Spitzbergen; Connecticut and Virginia, U.S.A.; South Africa (Karroo Formation); and New South Wales, Australia (Hawkesbury Formation). The typically Palaeozoic groups of *Elasmobranchii* having almost or completely passed away, the *Hybodontidae* begin to be numerous (*Hybodus* and *Acrodus*), and may be regarded as the early ancestors of the modern sharks. The *Dipnoi* are represented by *Ceratodus*, which differs little from the *Neoceratodus* which now survives in the rivers of Queensland. Of the *Crossopterygii* only the *Coelacanthidae* remain. The *Chondrostei* still include several *Palaeoniscidae*, and they are accompanied by the *Catopteridae*, which connect them with the higher groups; but the most characteristic Triassic *Chondrostei* are the specialised *Belonorhynchidae*, which are very widely distributed in Europe, Spitzbergen, Canada, and Australia. The *Protospondyli* are now numerous, represented especially by the primitive *Colobodontidae* and the *Semionotidae*, but including the first of the *Pycnodontidae* (*Eomesodon*) and some *Macrosemiidae* and *Eugnathidae*. The *Halecostomi* first

appear with the *Pholidophoridae*, which seem to be directly ancestral to the modern *Teleostei*. Some of the Triassic fishes, indeed, begin to show a marked tendency towards the ossification of the internal skeleton at the expense of the external armour.

The fish fauna of the **Lias** is a direct continuation and further development of that of the Trias. The majority of the known species occur in a remarkable state of preservation in the Lower Lias of Lyme Regis in Dorset, and of other localities in southern England. Few fishes are found in the Middle Lias; but they become numerous again in the Posidonomya shales and bituminous limestones of the Upper Lias ϵ in Würtemberg and Franconia, as well as in the corresponding strata of Werther, near Halle, the Departments of Calvados, Yonne, and Côte-d'Or in France, and of Ilminster and Whitby in England. The *Elasmobranchii* are represented by several species of *Hybodus* and *Acrodus* of the family *Hybodontidae*, and by one genus, *Palaeospinax*, which seems to be a forerunner of the *Cestraciontidae*. There are also the first typical *Holocephali*, of the primitive families *Squaloraiidae* and *Myriacanthidae*. The *Dipnoi* are unknown in Europe, but *Ceratodus* occurs in corresponding Lower Jurassic formations in Colorado and Wyoming, U.S.A. The *Coelacanthidae* alone represent the *Crossopterygii*. Among *Chondrostei* the *Palaeoniscidae* and *Belonorhynchidae* are now rare, but the family *Chondrosteidae*, from both the Lower and the Upper Lias, includes large fishes which are intermediate between the *Palaeoniscidae* and the modern sturgeons. The majority of the Liassic fishes, however, are Ganoids of the Order *Protospondyli*: especially characteristic and widespread is the deep-bodied, regularly scaled *Dapedius*. Only a single Pycnodont genus (*Eomesodon*) is known. Some of the *Protospondyli* have thin scales and considerable ossification of the internal skeleton (*Caturus* and *Pachycormidae*), while the *Halecostomi* comprise not only numerous *Pholidophoridae* but also, in the Upper Lias, the earliest *Leptolepidae*, which are very closely related to the primitive *Teleostei* of later date.

The **Dogger** or **Brown Jura** of Germany, and the corresponding **Lower Oolites** of England, usually contain only detached teeth, fin spines, bones, and scales of fishes, which resemble partly those of the Lias, partly those of the Upper and Middle Jurassic. Some of the teeth of the *Hybodontidae* are very similar to those of the earliest *Notidanidae*, which appear in the Middle Jurassic. Most of the dental plates of *Holocephali* seem to belong to the *Chimaeridae*. Small teeth of the Dipnoan *Ceratodus* are rare. Numerous jaws of *Pycnodontidae* represent chiefly the primitive genus *Eomesodon*. The earliest fragments of *Aspidorhynchidae* have been recognised. The **Middle** and **Upper Jurassic** fishes are numerous and well preserved in the Oxford and Kimmeridge Clays and the Portland Limestones of southern England, northern France, and Switzerland; and in the Lithographic Stone of Solenhofen, Kelheim, and Eichstädt in Bavaria, Nusplingen in Würtemberg, Cerin in Ain, France, and Vilanova de Meya in Lérida, N. Spain. The latest Jurassic fishes are also found well preserved in the Purbeck Beds of England and in the Wealden of England, Belgium, and northern Germany. The **Wealden** fishes are freshwater and estuarine survivals, which were in part contemporaneous with the marine fishes occurring in the Lower Cretaceous Neocomian strata. In the Middle and Upper Jurassic fauna the *Hybodontidae* include *Asteracanthus*, and are accompanied by more modernised *Cestraciontidae* and true *Notidanidae*, besides *Squatinidae* and certain *Rhinobatidae*, which may

be regarded as ancestral to the later skates. There are also forerunners of the modern *Spinacidae* and *Scylliidae*. *Holocephali* of the family *Chimaeridae* are common, and there is at least one survivor of the *Myriacanthidae*. The Crossopterygian *Coelacanthidae* now attain their greatest development, and the Chondrostean *Palaeoniscidae* are almost extinct, though small species of one genus, *Coccolepis*, survive as late as the Purbeck and Wealden. All families of the *Protospondyli* and *Halecostomi* are especially abundant and varied; among them the *Amiidae* and *Oligopleuridae* appear for the first time. It is the Age of Actinopterygian Ganoids.

With the beginning of the **Cretaceous** period there is an important change in the fish fauna, so that the previously dominant Ganoids become more and more displaced by Teleosteans. In the marine **Neocomian** formations of France, Germany, and Switzerland, which are probably contemporaneous with part of the estuarine Wealden deposits, the fragmentary remains of fishes belong chiefly to Hybodont sharks, Pycnodonts, and *Lepidotus*, but include a few teeth which represent the earliest predaceous sharks of the modern family *Lamnidae*. In the Voirons, Switzerland, there are good skeletons of the earliest Chirocentrids (*Spathodactylus*) and Clupeoids (*Crossognathus* and probably *Diplomystus*). In the limestones of Castellamare and Pietraroja near Naples, the Jurassic types of Ganoids also predominate, though they are mingled with a few true Clupeoids. In the limestones of the Isle of Lesina, Dalmatia, Teleosteans predominate and include, besides several Clupeoids, both forerunners of the *Acanthopterygii* and a few members of this modern Order (a Berycoid and *Aipichthys*). In the **Upper Cretaceous** formations of the Old World, such as the limestones of Mount Lebanon, the marly sandstones of Westphalia, and the White Chalk of England, N. France, and S. Sweden, only a few specialised survivors of the Jurassic Elasmobranchs and Ganoids occur, and the large majority of the fishes are Teleosteans, including several *Acanthopterygii*, chiefly Berycoids. In the New World the distribution of the Cretaceous fishes is much the same. In a Lower Cretaceous estuarine deposit at Bahia, Brazil, and in the marine Neocomian of Mexico and the United States, the Ganoids predominate; while in the Upper Cretaceous laminated chalk of the Niobrara Group in Kansas, well-preserved portions of skeletons of modern Elasmobranchs and Teleosteans constitute the whole known fauna. Well-preserved fishes occur in nodules in an Upper Cretaceous formation in Ceará, Brazil, and there are traces of a similar fish fauna in Queensland, Australia.

Among Upper Cretaceous *Elasmobranchii* the *Lamnidae* are especially abundant, including the extinct genus *Corax* (probably an ancestor of *Selache*), *Oxyrhina*, *Lamna*, and *Scapanorhynchus*, which seems to be identical with the existing deep sea genus *Mitsukurina*. There are also *Notidanidae*, *Cestraciontidae*, *Scylliidae*, *Spinacidae*, *Pristiophoridae*, *Squatinidae*, *Pristidae*, *Rhinobatidae*, and an extinct skate *Ptychodus*, which is the characteristic Elasmobranch of the period. These families do not always occur all together, and *Ptychodus* has not been found in the best known fish faunas of Mount Lebanon. The *Pristidae* are ancestral types (*Sclerorhynchus*, *Onchopristis*), in which the teeth of the rostrum or saw are not yet sunk in sockets. *Carchariidae* are absent. The *Holocephali* closely resemble those of the Jurassic period and include some of the largest known species (*Edaphodon*). The *Dipnoi* are represented solely by some small teeth of *Ceratodus* in N. Africa, Patagonia, and Australia.

The Crossopterygian family *Coelacanthidae* appears for the last time in Europe and Syria (*Macropoma*). The *Protospondyli* are represented by specialised or senile forms of *Semionotidae*, *Pycnodontidae*, *Eugnathidae* (*Neorhombolepis*), *Macrosemiidae*, *Aspidorhynchidae*, and *Pachycormidae* (*Protosphyraena*). Among Teleosteans the Clupeoids and Chirocentrids are especially varied, and there are several genera related to the *Scopelidae*, which seem to be the ancestors of fishes at present living in the deep sea. There are also genera of the deep sea *Halosauridae*. A few eels make their first appearance, some (*Urenchelys*) still retaining a caudal fin, at least one also with pelvic fins (*Anguillavus*). The *Acanthopterygii* are remarkably numerous, but are almost exclusively Berycoids and Carangoids. In the highest horizons of the Cretaceous (Montian) there are Percoids in N. France and India. The occurrence of *Lepidosteus* in India is interesting.

With the beginning of the **Tertiary** period there is a still closer approximation to the fish fauna of the present day. Among *Elasmobranchii* the *Cestraciontidae* are now represented only by *Synechodus*, which soon becomes extinct, and by *Cestracion*, which still exists locally. The *Dipnoi* have retreated to the freshwaters of the regions they still inhabit. Of the *Crossopterygii* only a few Polypterid scales are known from Egypt. Of the typically Mesozoic Ganoids, two Pycnodonts (*Pycnodus*, *Palaeobalistum*) alone survive, and these become extinct at the end of the Eocene. Of the higher Ganoids there are only *Lepidosteus*, *Amia*, and the Acipenseroids, as in the existing fauna, though the two former are not yet restricted to the freshwaters of North America. The modern sharks, skates, and bony fishes predominate, and are almost as varied as those in existing seas, only the geographical distribution of some of the tropical and sub-tropical families extends to northern regions which are now temperate. There must, indeed, have been very rapid evolution between the latest Cretaceous episode and the earliest Tertiary episode which has hitherto been found satisfactorily recorded among fossils.

The oldest Tertiary fishes are represented merely by fragments, chiefly teeth and otoliths, in the basement beds of the **Eocene** (often termed **Paleocene**) of western Europe and Africa. The first important marine fauna occurs in the **Lower Eocene** London Clay of England and its equivalents in France and Belgium. Among sharks the *Carchariidae* now appear for the first time; and the large rays of the family *Myliobatidae* are numerous. Among *Chimaeridae*, *Edaphodon* still survives. There are scutes of *Acipenser* and jaws of *Pycnodus*. *Siluridae* also appear, and peculiar Labroid fishes with a pharyngeal dentition named *Phyllodus*—a typical Lower and Middle Eocene fossil. The *Scombridae* are especially numerous, and there are some primitive *Xiphiidae*, besides the curious Xiphioid *Cylindracanthus*. Skulls apparently of *Scorpaenidae* and *Gadidae* also occur, and there are remains of many other specialised *Teleostei*. The *Acanthopterygii* now much outnumber the physostomous *Teleostei*. **Middle** and **Upper Eocene** fishes are represented by fragments in deposits above the London Clay in western Europe, on the German Baltic coast, in Persia, Egypt, Tunis, and Nigeria. *Amia* and *Lepidosteus* occur in Europe, and large *Siluridae* are especially numerous in Egypt. The Upper Eocene fauna is represented by a very numerous and varied assemblage of well-preserved fishes in the fissile limestone of Monte Bolca, near Verona. Almost all groups which at the present day inhabit the shallower waters of tropical seas occur here, with

the last species of *Pycnodus* and *Palaeobalistum* and a peculiar Xiphioid *Blochius*, which is closely allied to *Cylindracanthus*.

Fragments of nearly similar Eocene fishes, especially teeth of *Elasmobranchii*, are found in certain marine deposits near the eastern coast of the United States of America; but most of the known deposits containing Eocene fishes in North America are of freshwater origin, and so exhibit another phase of fish life. The Green River Shales of Wyoming yield fine specimens of a freshwater sting ray (*Xiphotrygon*), a *Lepidosteus*, *Clupeidae* (*Diplomystus*), *Osteoglossidae* (*Phareodus*), *Chromidae* or *Cichlidae* (*Priscacara*), and some Percoids. Other contemporaneous formations in the West also contain *Lepidosteus*, *Amia*, and *Siluridae*.

The earliest **Oligocene** fishes occur in the black slates of Matt in Canton Glarus, the contemporary Menilite Shales of Styria, Upper Bavaria (Siegsdorf), Upper Alsace, and other localities. The well-preserved fishes of Glarus are all *Teleostei* adapted for the deep sea, and most of them belong to extinct genera. *Lepidopus* is especially common. Later Oligocene fishes are found chiefly as fragments in the Rupelian Clay of Belgium and in sandy deposits in the Mainz and Paris basins. A few nearly complete specimens, however, are obtained from the Septarian Clay of Mainz. The Oligocene marine fauna in Europe is still tropical or sub-tropical, and is directly continuous with that of the Eocene. Freshwater Percoids, *Amia*, and other fishes are found in the Oligocene of Provence.

In the **Lower Miocene** of Messel, near Darmstadt, *Lepidosteus* and *Amia* occur for the last time in Europe. Freshwater fishes are also well preserved in the lignite of Rott, near Bonn, and in contemporaneous deposits in Bohemia. The **Middle Miocene** Molasse of Switzerland, Würtemberg (Baltringen), and Upper Bavaria, the marine deposits of the Vienna basin, the valley of the Rhine, and the Aquitaine basin, sometimes contain an abundance of fish remains, among which the teeth, dermal plates, and spines of sharks, rays, and chimaeras, the vertebrae, teeth, and scattered bones of *Teleostei* are especially common. With few exceptions these remains are referable to recent genera. The brackish-water clay of Unterkirchberg, near Ulm, the freshwater marl of Oeningen and Steinheim, the Sarmatian deposits of Radoboj and other localities in Croatia, and the *Cerithium* marl of the Vienna basin, also show that at the time of their formation the fish fauna of the fresh and brackish waters of Germany was not very different from that still surviving in southern Europe and Asia Minor. The **Upper Miocene** marine fauna is well represented at Licata in Sicily, in the neighbourhood of Girgenti, in the gypseous marls of Sinigaglia, near Gabbro in Tuscany, Lorca in Spain, and Oran in Algeria. It is essentially a Mediterranean fauna, but without exception the species are extinct. So far as fishes are concerned, there is scarcely any noteworthy difference between the **Pliocene** fauna and that of the present day. Some of the sharks of the family *Lamnidae* attained a large size, and gigantic teeth of *Carcharodon* and *Oxyrhina* characterise Miocene and Pliocene formations in many parts of the world. They are also sometimes dredged from the bottom of the present deep sea.[1]

The distribution of the **Pleistocene** fish fauna in the northern hemisphere

[1] *Eastman, C. R.*, Sharks' Teeth and Cetacean Bones from the Red Clay of the Tropical Pacific. Mem. Mus. Comp. Zool. Harvard, vol. xxvi., no. 4, art. v, 1903; also Bull. Mus. Comp. Zool. Harvard, vol. l., no. 4, 1906.

was probably affected by the glacial conditions of the time, but little is known about it. In this connection the occurrence of the northern Capelin (*Mallotus villosus*) in Bosnia is interesting.

Class 2. AMPHIBIA. Amphibians or Batrachians.[1]

Cold-blooded aquatic or terrestrial vertebrates, usually naked, but sometimes with a horny or bony dermal covering; respiration both by gills and by lungs in early stages, and in some forms gills remain functional throughout life. Heart with one ventricle and two auricles. Development without amnion and allantois, by metamorphosis. Skull usually with two occipital condyles. Generally a single sacral vertebra. Limbs adapted for walking or swimming, never in the form of fins, and rarely absent.

In external appearance Amphibians more nearly resemble Reptiles than Fishes. The body is generally elongate, and terminates as a rule in a well-developed tail, although some small forms (*Anura*) are tail-less. Among recent Amphibians limbs are wanting only in the Coecilians (*Gymnophiona*). Certain extinct Stegocephalians (*Dolichosomidae*) appear also to have been completely limbless; but elsewhere two pairs of limbs are invariably present, the anterior usually terminating in four digits and the posterior in five.

Recent Amphibians are naked with the exception of the Coecilians, which are covered with small scales arranged in transverse rings, and certain frogs (*e.g. Ceratophrys*), which have some ossifications in the skin of the back. The fossil Stegocephalians usually have a scaly armature on the ventral surface, and sometimes also on the back. Sense organs of the lateral line system, like those of Fishes, are well developed in the aquatic forms, and also occur in the larvae of the land forms.

The number of vertebrae in the spinal column is extremely variable (10-150), depending on the length of the body and especially the tail. Cervical, dorsal, sacral, and caudal regions are distinguishable.

The most primitive form of vertebrae occurs in the Palaeozoic Stegocephalians, where the notochord is enclosed by thin cylinders of bony tissue, or by separate pleurocentra and hypocentra, as in early Ganoids. Where the column is more extensively ossified, as in the existing Amphibians, three types of vertebrae are exhibited. The first, or *amphicoelous*, is biconcave; the *procoelous* has the anterior vertebral face concave and the posterior convex; and the *opisthocoelous* has the anterior face convex, the posterior concave.[2]

The cervical region comprises but a single vertebra, the atlas, although this probably corresponds to both atlas and axis of higher Classes. Its concave anterior face receives the bony or cartilaginous occipital condyles, and is often provided with a spatulate, forwardly directed basal process. Each of the dorsal vertebrae supports a neural arch (*neurapophysis*), which becomes earlier and more extensively ossified than the centrum, and may be either suturally united or anchylosed with the latter. The two halves of the neural arch unite above to form a more or less strongly developed spinous process (*spina dorsalis*); and they bear anteriorly and posteriorly a pair of oblique

[1] *Hoffmann, C. K.*, Die Amphibien. Bronn's Classen und Ordnungen des Tierreichs, vol. vi., pt. 2, 1873-78.—*Wagner, J.*, Natürliches System der Amphibien, 1828-33.

[2] *Nopcsa, F.*, Über prozöle und opisthozöle Wirbel. Anat. Anzeig., vol. lxix., p. 19, 1930.

articular processes (*processus obliqui*, *zygapophyses*), the forward pair of each vertebra overridden by the hinder pair of the next in front. Sometimes, as in the Stegocephalians *Diplocaulus* and *Sauropleura*, the articulation is further strengthened by a process between the prezygapophyses (*zygosphene*) fitting into a pit between the postzygapophyses (*zygantrum*). The neural arch also supports, as a rule, a pair of transverse processes (*diapophyses*) for the attachment of ribs. When the ribs are double-headed, as is often the case, another and shorter lateral process (*parapophysis*) is developed by the centrum. In existing Amphibians the ribs are short and never reach the sternum. In the extinct Stegocephalians they are usually long and curved, encircling the body cavity.

The sacral region is usually formed by a single vertebra, which supports the pelvis, the latter being attached either directly by means of exceptionally stout transverse processes, or by sacral ribs, usually of peculiar form. Haemal arches (*haemapophyses*, "chevron bones") are commonly borne by the caudal series, the foremost of which sometimes have ribs attached to the transverse processes of the neural arch. The entire series of caudals in the *Anura* is fused into a single elongate piece called the *coccyx*.

The primordial *cranium* remains partly cartilaginous throughout life, and is partly replaced by bony pieces, which are either direct ossifications of the cartilaginous capsule (exoccipitals, auditory capsules, quadrate, sphenethmoid), or are investing bones (parietals, frontals, nasals, vomer, parasphenoid). The basioccipital and supraoccipital usually remain small cartilaginous tracts; but except in certain *Stegocephali* and a few other forms, the exoccipitals are completely ossified and bear the articular condyles. The exoccipitals are of considerable size, and enter into the border of the otic region. The latter is enclosed by small bones corresponding to the prootic and opisthotic of fishes, or these may unite into a single element called the petrosal. The anterolateral walls of the skull remain cartilaginous; but in the ethmoidal region an ossification takes place, forming the "orbitosphenoid" which is usually separate, but sometimes (*Anura*) fuses with the median elements to form a single ring-shaped bone (sphenethmoid).

The cranial roof is formed by the paired parietals, frontals, pre- and post-frontals, and nasals; and in Stegocephalians there are present in addition an occipital row of paired postparietals and tabulars, besides the supratemporals, intertemporals, squamosals, postorbitals, and lachrymals. A pair of small membrane bones, the septomaxillaries, also occur in the border of the narial openings.[1] The palate is formed as in fishes by a large median parasphenoid, and usually a paired vomer. There is no movable suspensorium for the lower jaw; the cartilage representing it unites with the squamosal above and quadrato-jugal below. Sometimes an ossified quadrate is formed at the end of the suspensorial cartilage. Attached to the quadrato-jugals in front are the maxillae, and anterior to these the premaxillae, which complete the rim of the upper jaw in front. Many of the Urodeles have the maxillae and quadrato-jugals replaced by connective tissue. Between the quadrate and parasphenoid is placed the pterygoid, usually a trifid bone which joins the parasphenoid by its shorter arm, while its anterior branch forms the outer border of the palatal (or interpterygoid) vacuity. The palatines, when present, usually join the

[1] *Wegner*, *R. N.*, Der Stützknochen, Os Nariale, in der Nasenhöhle. Morphol. Jahrb., vol. li., p. 413, 1922.

anterior ends of the pterygoids, and extend parallel with the maxillae. The mandibular ramus is composed of three or more elements, as in fishes. The visceral skeleton is formed by the paired hyoid bones, and, in gill-breathers, by three or four partially ossified branchial arches.

The *teeth* are acutely conical, and are commonly borne by the mandible, maxillae, premaxillae, vomers, and palatines. Rarely the parasphenoid and pterygoid are armed with minute teeth, and only certain *Anura* are toothless. Teeth of the *acrodont* type have their bases implanted directly in the rim or top of the jaws; those of the *pleurodont* type are sunk against the inner side of the jaws. As in Ganoids and bony fishes, worn teeth are not replaced by successors developed beneath them, but new teeth are formed independently alongside the old, and gradually oust the latter as their basal parts become absorbed. Amphibian teeth differ from those of fishes chiefly in the absence of vasodentine; and the spacious pulp cavity, which during life contains vascular or connective tissue, occurs in the fossil state either hollow or filled with mineral matter. Some Stegocephalians have complex or "labyrinthodont" teeth, the dentine being strongly folded, and almost or completely obliterating the pulp cavity, as in certain Crossopterygian fishes.

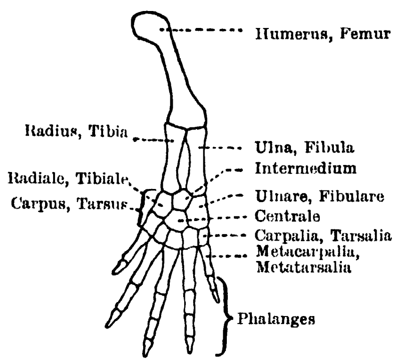


Fig. 276.
Diagram of the bones of the fore or hind limb of a primitive Land Vertebrate. After Gegenbaur.

In the *pectoral arch* the scapula is ossified in at least its proximal portion, where it joins the coracoid and precoracoid, and forms the articular face for the humerus. A bony sternum is usually absent. Stegocephalians are peculiar in possessing between the pectoral limbs one median and two paired exoskeletal plates, commonly regarded as interclavicle and clavicles, sometimes with cleithra above. The fore limb (Fig. 276) is composed of the usual bones, humerus, radius, and ulna; a carpus which is either cartilaginous or consists of two rows of ossicles with from one to four separate centralia; and three, four, or five metacarpals which support digits with from one to three phalanges in existing Amphibians, often more in the extinct Stegocephalians.

The *pelvic arch* is composed of a long and slender bony ilium, which is attached either directly to the transverse process of the sacral vertebra, or to the sacral rib, and is directed obliquely downward; a flattened, sometimes discoidal bony ischium; and a cartilaginous or ossified pubis lying immediately in advance of the ischium. The ilium and ischium usually take part together in the formation of the acetabulum, which receives the head of the femur. In the *Anura* the tibia and fibula are fused. The tarsus is cartilaginous or composed of several small ossicles, and the pes resembles the manus, except that it is usually pentadactyl.

Four Orders of Amphibians are recognised as follows:—*Stegocephali*, *Gymnophiona*, *Urodela*, and *Anura*.

Order 1. STEGOCEPHALI.[1]

Salamander- or lizard-like tailed Amphibians, the cranial roof and usually the whole of the cheek covered with plates; pineal foramen always occurring in the parietal. Teeth sharply conical, and the walls of the pulp cavity sometimes highly complicated by infolding of the dentine. Vertebrae consisting either of simple cylinders, or of separate pleurocentra and hypocentra (intercentra), or of completely ossified amphicoelous centra. Three exoskeletal plates present in the thoracic region, interpreted as clavicles and interclavicle. Usually a ventral and sometimes a dorsal armouring of small overlapping scales.

[1] *Ammon, L. v.*, Die permischen Amphibien der Rheinpfalz. Munich, 1889. [Extensive bibliography.]—*Baur, G.*, The Stegocephali: a Phylogenetic Study. Anat. Anzeig., vol. xi., p. 657, 1896.—*Branson, E. B.*, Structure and Relationships of American Labyrinthodontidae. Journ. Geol., vol. xiii., p. 568, 1905.—*Branson, E. B.*, and *Mehl, M. G.*, Auditory Organs of Some Labyrinthodonts. Bull. Geol. Soc. Amer., vol. 39, p. 485, 1928.—*Broili, F.*, Permische Stegocephalen und Reptilien aus Texas. Palaeontographica, vol. li., p. 1, 1904.—Unser Wissen über die ältesten Tetrapoden. Fortschr. naturwiss. Forschung, vol. viii., 1913.—*Case, E. C.*, Revision of the Amphibia and Pisces of the Permian of North America. Carnegie Inst. Washington, publ. no. 146, 1911.—The Environment of the Amphibian Fauna at Linton, Ohio. Amer. Journ. Sci., vol. xliv., p. 124, 1917.—Permo-Carboniferous Red Beds of N. America and their Vertebrate Fauna. Carnegie Inst. Washington, publ. no. 207, 1915.—Permo-Carboniferous Conditions versus Permo-Carboniferous Time. Journ. Geol., vol. xxvi., p. 500, 1918.—New Reptiles and Stegocephalians from the Upper Triassic of Western Texas. Carnegie Inst. Washington, publ. no. 321, 1922.—*Case, Williston*, and *Mehl*, Permo-Carboniferous Vertebrates from New Mexico. Carnegie Inst. Washington, publ. no. 181, 1913.—*Cope, E. D.*, Synopsis of the extinct Batrachia and Reptilia of North America. Trans. Amer. Phil. Soc., vol. xiv., 1869.—*Ibid.* n.s., vol. xvi., 1886.—Batrachia of the Permian Period of North America. Amer. Nat., vol. xviii., 1884.—Synopsis of Extinct Batrachia from the Coal Measures. Geol. Surv. Ohio, Palaeontology, vol. ii., p. 351, 1875.—*Credner, H.*, Die Stegocephalen aus dem Rothliegenden bei Dresden. Parts. I.-X. Zeitschr. Deutsch. Geol. Ges., 1881-93.—Die Urvierfüssler (Eotetrapoda) der Sächsischen Rothliegenden. Berlin, 1891.—*Fritsch, A.*, Die Fauna der Gaskohle und der Kalksteine der Permformation Böhmens, vols. i.-iii., 1883-94.—*Fürbringer, M.*, Zur vergleichenden Anatomie des Brustschulterapparates und der Schultermuskeln. Jena. Zeitschr., vol. xxxiv., p. 215, 1900.—*Haughton, S. H.*, Descriptive Catalogue of the Amphibia of the Karroo System. Ann. S. African Mus., vol. xxii., p. 227, 1925.—*Huene, F. von*, Skull Elements of the Permian Tetrapoda. Bull. Amer. Mus. Nat. Hist., vol. xxxii., p. 315, 1913.—*Huxley, T. H.*, Vertebrate Remains from Kilkenny. Trans. Roy. Irish Acad., vol. xxiv., 1867.—*Jaekel, O.*, Neues über Hemispondyla. Palaeont. Zeitschr., vol. v., p. 1, 1922.—*Meyer, H. von*, and *Plieninger, T.*, Beiträge zur Paläontologie Württembergs. Stuttgart, 1844.—*Miall, L. C.*, Report on the Structure and Classification of the Labyrinthodonts. Rep. Brit. Assoc., 42nd and 43rd Meet., 1874-75.—*Moodie, R. L.*, Lateral Line System in Extinct Amphibia. Journ. Morphol., vol. xix., p. 511, 1908.—The Coal Measures Amphibia of North America. Carnegie Inst. Washington, publ. no. 238, 1916.—*Nopcsa, F.*, Notes on Stegocephalia and Amphibia. Proc. Zool. Soc., 1930, p. 979, 1931.—*Romer, A. S.*, Vertebrate Faunal Horizons in the Texas Permo-Carboniferous Red Beds. Univ. Texas Bull. 2801, p. 67, 1928.—The Pennsylvanian Tetrapods of Linton, Ohio. Bull. Amer. Mus. Nat. Hist., vol. lix., p. 77, 1930.—*Steen, M. C.*, Amphibia from the Middle Coal Measures of Linton, Ohio, U.S.A. Proc. Zool. Soc., 1930, p. 849, 1931.—*Sushkin, P. P.*, Modifications of the Mandibular and Hyoid Arches . . . in the Early *Tetrapoda*. Palaeont. Zeitschr., vol. viii., p. 263, 1927.—*Thevenin, A.*, Amphibiens et reptile du terrain houiller de France. Ann. Paléont., vol. i., p. 145, 1906.—Les plus anciens quadrupèdes de France. *Loc. cit.*, vol. v., p. 1, 1910.—*Watson, D. M. S.*, Brain-case in certain Lower Permian Tetrapods. Bull. Amer. Mus. Nat. Hist., vol. xxxv., p. 611, 1916.—Structure, Evolution, and Origin of the Amphibia.—The "Orders" Rachitomi and Stereospondyli. Phil. Trans. Roy. Soc., vol. 209B, no. 360, 1919.—Evolution and Origin of the Amphibia. *Loc. cit.*, vol. 214B, no. 416, 1926.—Carboniferous Amphibia of Scotland. Palaeont. Hungarica, vol. i., p. 221, 1930.—*Williston, S. W.*, Primitive Structure of Mandible in Reptiles and Amphibians. Journ. Geol., vol. xxii., p. 410, 1914.—Restorations of some American Permo-Carboniferous Amphibians and Reptiles. *Loc. cit.*, vol. xxii., p. 57, 1914.—Synopsis of American Permo-Carboniferous Tetrapoda. Contrib. Walker Mus. Chicago, vol. i., no. 9, p. 193, 1916.—*Wiman, C.*, Hinterhaupt der Labyrinthodonten. Bull. Geol. Inst. Upsala, vol. xii., p. 1, 1913.

The Stegocephalians range from the Lower Carboniferous to the Upper Trias, and comprise the largest known Amphibians. A tail is invariably present, and in most cases there are two pairs of limbs; only a few genera are apparently destitute of limbs.

Unlike recent Amphibians, most *Stegocephali* possess a well-developed dermal armour of bony scales or scutes, which almost always covers the ventral surface of the body, and sometimes also extends to the under side of the limbs and the back (Fig. 277). The ordinary dorsal scales are thinner than the abdominal scales, and are usually round or oval, but they are sometimes accompanied by thick sculptured plates, which are fixed to the expanded upper ends of the neural spines (Fig. 278). The ventral scutes are sometimes thickened, and always arranged in regular series. The abdominal series form oblique rows converging forwards at a sharp angle along the median line, but those covering the thoracic, pectoral, and caudal regions, and under side of the limbs are arranged in different patterns. The scales are of true bony tissue, and vary considerably in form, the more common varieties being oval, rhomboid, hexagonal, oblong, fusiform, or rod-shaped (Fig. 277).[1]

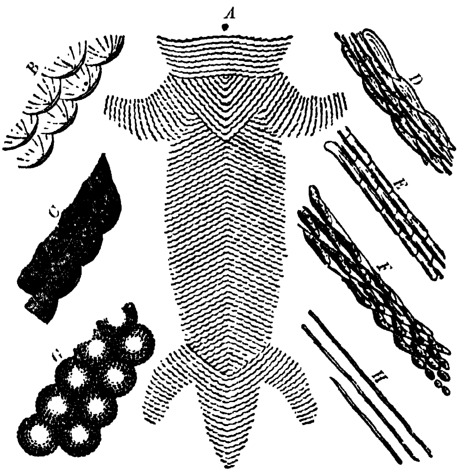


FIG. 277.

A, Ventral armour of *Branchiosaurus*; *B*, scutes of *Branchiosaurus*; *C*, of *Hylonomus*; *D*, of *Pelosaurus*; *E*, of *Archegosaurus*; *F*, of *Sclerocephalus*; *G*, of *Discosaurus*; *H*, of *Petrobates* (after Credner).

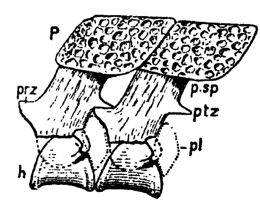


FIG. 278.

Two dorsal vertebrae of *Aspidosaurus chiton* Broili, supporting dermal plates. Permian; Texas. *h*, hypocentrum; *pl*, pleurocentrum (restored); *p.sp*, spinous process; *prz*, prezygapophysis; *ptz*, postzygapophysis; *P*, ornamented dermal plate. Somewhat magnified (after Broili).

The *vertebral column* usually remains in an embryonic condition, and recalls that of Ganoid fishes. The degree of persistence of the notochord is very variable, but only the most specialised genera have it completely interrupted by ossification of the centra; in the *Phyllospondyli* (*Branchiosauridae*) it is completely persistent.

Ossification of the vertebral column is least extensive among the *Phyllospondyli* (Figs. 279, 280), where, in the absence of pleurocentra, the neural arch itself extends downward and joins a pair of delicate hypocentra (or intercentra) to enclose the notochord and to form transverse processes for support of the ribs. In the *Lepospondyli* (Fig. 281) the notochord is persistent and encased in constricted bony cylinders, which are hourglass-shaped in longitudinal section. In some genera, however, the continuity of

[1] *Broili, F.*, Hautbedeckung der Archegosauridae und Actinodontidae. Zeitschr. Deutsch. Geol. Ges., vol. lxxix., Abh. p. 375, 1927.

the chord is all but interrupted by ossification of the middle portion of the centra.

The *Temnospondyli*[1] at first have the vertebrae composed of several distinct pieces. Ossification begins with the neural arch, whose halves remain separate

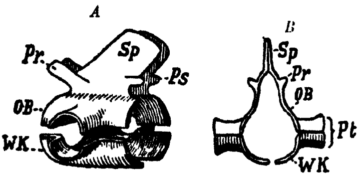


Fig. 279.

Phyllospondylous dorsal vertebra of *Branchiosaurus*, in side view (*A*), and in front view (*B*). *OB*, neural arch; *Pr*, prezygapophysis; *Ps*, postzygapophysis; *Pt*, transverse process; *Sp*, neural spine; *WK*, hypocentra. Much magnified (after Credner and Thevenin).

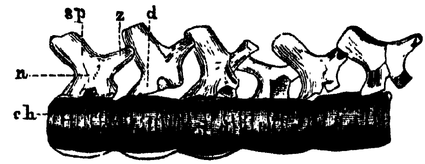


Fig. 280.

Phyllospondylous vertebrae of *Branchiosaurus amblystomus* Credner. Magnified (after Credner). *ch*, notochord; *d*, transverse process; *n*, neural arch; *sp*, neural spine; *z*, zygapophysis.

at first, but later coalesce and are continued above into a stout and sometimes distally thickened spinous process. The centra may be either *embolomerous*, *rhachitomous*, or *stereospondylous*. Those of the embolomerous type consist each

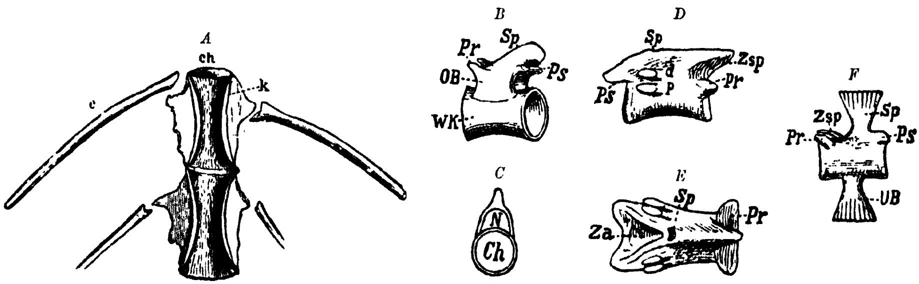


Fig. 281.

Lepospondylous vertebrae. *A*, Two vertebrae of *Hylonomus* in horizontal longitudinal section, showing cavity for notochord; *B*, *C*, dorsal vertebra of *Hylonomus* in side view and cross-section; *D*, *E*, dorsal vertebra of *Diplocaulus* in side view and from above; *F*, caudal vertebra of *Urocordylus* in side view. *c*, rib; *Ch*, space for notochord; *d*, diapophysis of transverse process; *N*, space for spinal chord; *p*, parapophysis of transverse process; *UB*, haemal arch; *WK*, centrum; *Za*, zygantrum; *Zsp*, zygosphene; other letters as in Fig. 279. *A*, after Credner; *B*-*E* after Broili; *F*, after Schwarz. Much magnified, except *D*, *E*, about 1/2 nat. size.

of two complete rings or perforated discs, of which the anterior (*hypocentrum* or *intercentrum*) bears the neural and haemal arches, while the posterior (*pleurocentrum*) is without arches or only shares the support of the neural arch

[1] *Broili, F.*, Die Rhachitomen Wirbel der Stegocephalen. Zeitschr. Deutsch. Geol. Ges., vol. 60, Monatsb., p. 235, 1908.—*Cope, E. D.*, Intercentrum of the Terrestrial Vertebrata. Trans. Amer. Phil. Soc., vol. xvi., p. 243, 1886.—*Gadow, H.*, Evolution of the Vertebral Column of Amphibia and Amniota. Phil. Trans. Roy. Soc., vol. 187B, p. 1, 1896.—*Götte, A.*, Wirbelbau bei den Reptilien, etc. Zeitschr. f. wiss. Zool., vol. 62, p. 343, 1897.—*Huene, F. von*, Phylogenetische Bedeutung des Wirbelbaues der Tetrapoden. Palaeont. Zeitschr., vol. vii., p. 260, 1926.—*Jakovlev, N. N.*, Primary Factors in the Evolution of the Vertebral Column. Trav. Soc. Natural. Pétrograd, vol. i., p. 9, 1920.—*MacBride, E. W.*, Development of the Vertebral Column. Biol. Reviews (Cambridge), vol. vii., p. 108, 1932.—*Schwarz, H.*, Morphogenie der Wirbelsäule der Tetrapoden. Sitzb. Ges. naturf. Freunde, Berlin, 1908, p. 315.—Wirbelsäule und Rippen holospondyler Stegocephalen. Beitr. Geol. u. Paläont. Österr.-Ungarns, vol. xxi., p. 63, 1908.—*Williston, S. W.*, Significance of Hypocentra and Pleurocentra. Bull. Geol. Soc. America, vol. xxi., p. 265, 1910.—Development of Holospondylous Vertebrae. Journ. Geol., vol. xviii., p. 594, 1910.—Evolution of Vertebrae. Contrib. Walker Mus. Chicago, vol. ii., p. 75, 1918.

(Figs. 282, 283). Those of the rhachitomous type (Figs. 284, 285) are formed by a horseshoe-shaped basal piece (*hypocentrum* or *intercentrum*), the tapering extremities of which are directed upward, and a pair of lateral pieces, or *pleurocentra*; a structure which is paralleled in certain Ganoids (*cf.* Fig. 167). The hypocentrum usually ossifies in advance of the pleurocentra, and lies directly underneath the neural arch. Occasionally the pleurocentra are subdivided into two pairs, as in the anterior caudals of *Archegosaurus* (Fig. 284, *B*).

FIG. 282.
Three embolomerous vertebrae of *Diplovertebron punctatum* Fritsch. Lower Permian; Bohemia. Nat. size (after A. Fritsch).

The centra of the stereospondylous type lose the pleurocentra completely (or retain only occasional vestiges of them), while the intercentra form solid bony discs, sometimes perforated for the passage of the notochord.

There is usually but one cervical vertebra, the atlas (Fig. 286), which is concave in front and faceted to receive the occipital condyle or exoccipital condyles, but bears neither ribs nor anterior zygapophyses. Most or all of the presacral or dorsal series bear ribs, which may be either single- or double-headed. In most groups there is a single sacral vertebra provided with a pair of stout transverse processes for the attachment of sacral ribs; but in some of the primitive *Embolomeri* there appear to be two or three sacral vertebrae, with the slender ilia overlapping the sacral ribs. Haemal arches (haemapophyses, "chevron bones") are borne by the caudal vertebrae.

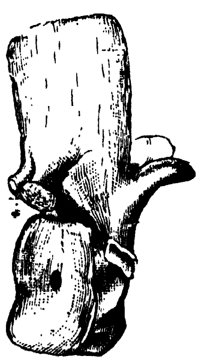


FIG. 283.
Intercentral disc of *Loxomma* bearing neural arch. English Coal Measures. 1/2 nat. size.

The *cranium* (Figs. 287-292) usually exhibits the depressed, broadly triangular form characteristic of Amphibians, but is completely covered with bony plates which are arranged very differently from those of modern Amphibians, and agree closely with those of the Palaeozoic Crossopterygian Ganoid Fishes. The cranial plates are usually ornamented externally with radiating sculpture, pittings, or punctae; and sensory canals are often conspicuous, one longitudinal pair forming the so-called *lyra* between the orbits and narial openings (see especially Figs. 311, 312, 316).

The cranial roof (Fig. 287) is pierced by several apertures, the largest of which are the orbits, and around them there is often a sclerotic ring. The anterior or external nares are placed close to the border of the snout, and separated from each other by a considerable interval. Another and smaller opening occurs at the median suture between the parietals, corresponding in position to the pineal foramen of Lizards.

The thin, flat bones constituting the cranial roof are of dermal origin, as in the cartilaginous Ganoids. The brain cavity is protected by the large, paired parietals (*P*), posterior to which are two pairs of bones corresponding with the supratemporals of fishes, the outer forming the inner and hinder angle of the otic or auditory notch (*Os*). The inner or median pair of supratemporals are now commonly described as postparietals or dermo-supraoccipitals (*PP*), and the outer or lateral pair as tabulars (*Tb*). The plate anterior to the tabular is usually called the supratemporal or suprasquamosal (*St*), and to the side and in front of this lies the large, posterior cheek plate (*S*), which is now

usually identified with the squamosal. The supratemporals, postparietals, and tabulars are wanting in all modern Amphibians. Anterior to the parietals and between the orbits is a pair of usually elongate narrow frontals (*F*), and anterior to these a pair of large nasals (*N*) with openings for the external

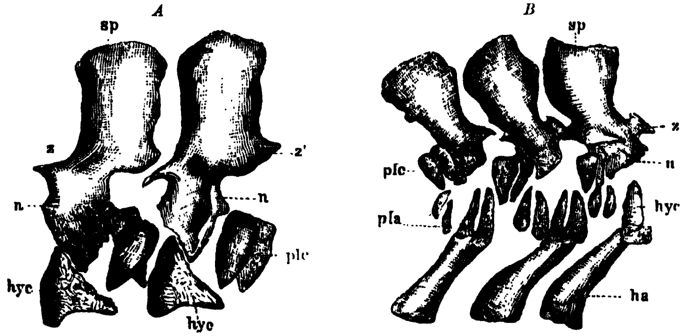


FIG. 284.

Rhachitomous vertebrae of *Archegosaurus*, dorsal (*A*) and caudal (*B*). Lower Permian; Germany. *ha*, haemal arch; *hyc*, intercentrum (hypocentrum); *n*, neural arch; *pla*, supplementary pleurocentra in caudal region; *plc*, pleurocentra; *sp*, neural spine; *z*, *z'*, zygapophyses. About nat. size.

nares at their antero-lateral angles (*Ch*). A pair of curved dentigerous premaxillae (*Pm*) terminate the snout in front.

The frontals rarely enter the border of the orbits. These openings are usually bounded behind by the postorbital (*Po*) and postfrontal, the latter plate being invariably present; mesially by the postfrontal (*Ptf*) and prefrontal

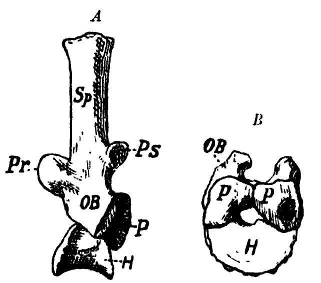


FIG. 285.

Rhachitomous vertebra of *Eryops*, in side view (*A*) and from behind (*B*). Permian; Texas. *H*, intercentrum (hypocentrum); *OB*, neural arch; *P*, pleurocentra; *Pr*, prezygapophysis; *Ps*, postzygapophysis; *Sp*, neural spine. About $1/2$ nat. size (after Broili).

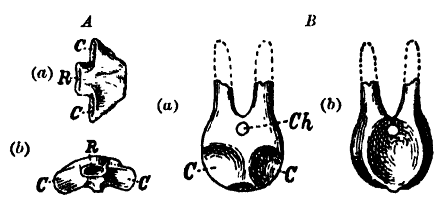


FIG. 286.

A, Atlas vertebra of *Diplocaulus*, from below (*a*) and in front (*b*), after Broili. *B*, atlas vertebra of *Dissorophus*, from in front (*a*) and behind (*b*), after Williston. *C*, facets for occipital condyles; *Ch*, canal for notochord; *R*, canal for spinal chord. About $1/2$ nat. size.

(*Prf*); and exteriorly by a long cheek plate called the jugal (*J*). Very often a narrow bone, the lachrymal (*L*), is inserted between the prefrontal and jugal, but it is usually pushed forward in advance of the orbit. The postero-inferior cranial angle is formed by the quadrato-jugal (*Qj*), and within it is a distinct quadrate bone. Joining the jugal or quadrato-jugal in front is the maxilla (*M*), a long, narrow, gently curved bone, which completes the outer border of the cranium as far as the premaxillae.

In the early Palaeozoic Stegocephalians the brain case seems to have been

comparatively well ossified, and in the genera in which the occiput has been observed there is a single concave occipital condyle, formed chiefly by the basioccipital, but partly also by the exoccipitals. Each exoccipital just reaches the vagus nerve in front and is pierced by a small foramen apparently for the exit of the hypoglossal nerve (*XII*) behind. The front part of the brain cavity lies in the upper part of a thick interorbital septum (Fig. 288). In the latest Triassic Stegocephalians (Figs. 289, 290) the basioccipital, basisphenoid, and supraoccipital are reduced and scarcely if at all ossified, and there is a pair of condyles formed solely by the exoccipitals. The vagus foramen is included within the exoccipital, and the hypoglossal nerve (*XII*) eventually passes out behind the skull. The front part of the brain cavity then extends downward to be floored by the parasphenoid, as in modern Amphibians.

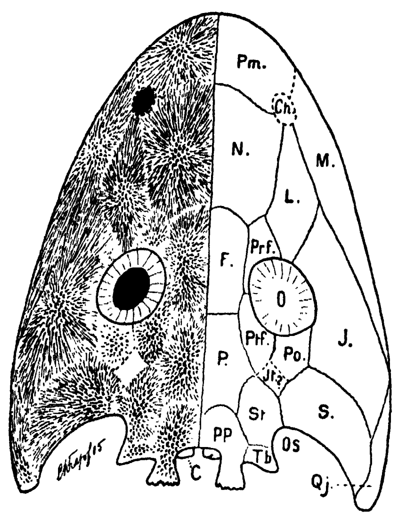


Fig. 287.

Cranial roof of *Cochleosaurus bohemicus* Fritsch. Lower Permian; Bohemia. *C*, occipital condyles; *Ch*, external nostril; *F*, frontal; *J*, jugal; *Jt*, supposed intertemporal; *L*, lachrymal; *M*, maxilla; *N*, nasal; *O*, orbit with sclerotic ring; *Os*, auditory notch; *P*, parietal; *Pm*, premaxilla; *Po*, postorbital; *pp*, postparietal; *Prf*, prefrontal; *Ptf*, postfrontal: *Qj*, quadrato-jugal; *S*, squamosal; *St*, supratemporal; *Tb*, tabular. About 1/2 nat. size (after Broili).

The under side of the cranium (Figs. 291, 292) is remarkable for the great development of the parasphenoid (*Psph*), which usually expands posteriorly into a broad, thin plate. It extends forwards as a long, slender bone (*cultriform process*), and unites with the relatively large vomer (*V*), the latter element being paired in the earlier, unpaired in the later forms. The vomer usually joins the premaxillae (*Pmx*) anteriorly, and is bounded exteriorly by the maxillae (*Mx*), the internal nares, and front portion of the palatines (*Pl*). Its broad, flat surface is either edentulous or set with minute teeth, but occasionally one or two powerful tusks are present in front of the narial openings, and there is a series of smaller teeth bordering the anterior and lateral edges of the vomer.

The pterygoids (*Pt*) are relatively large triradiate bones, which articulate with basipterygoid processes of the basisphenoid (*Bs*) in some of the earlier Stegocephalians (Fig. 291), with the edges of the hinder expansion of the parasphenoid in other and later forms (Fig. 292). The large forwardly directed ramus, which often extends to the vomer, is very broad in the most primitive early forms, reducing the interpterygoid vacuity to a narrow slit (Fig. 291); but it becomes narrower and shorter in the more specialised forms, and the interpterygoid vacuity is relatively wide (Fig. 292). Its short posterolateral ramus extends to the quadrate and quadrato-jugal. The palatines (*Pl*) adjoin the vomer and anterior extremities of the pterygoids. They are bordered externally by the maxillae, as a rule, and anteriorly by narial openings. They frequently bear teeth. A transverse (ectopterygoid) bone (*Tr*, Fig. 291) is sometimes distinguishable behind the palatine.

The lower jaw (Fig. 293) of nearly all *Stegocephali* extends the full

length of the skull, and in consequence the gape of the mouth is very wide, as in *Anura*. In complexity it approaches that of the Palaeozoic Crossopterygian

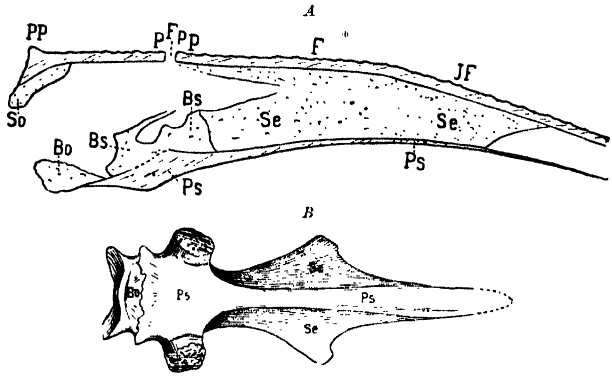


FIG. 288.

Median axis of skull of *Eryops megacephalus* Cope, in longitudinal section (*A*) and from below (*B*). Permian; Texas. *Bo*, basioccipital; *Bs*, basisphenoid; *F*, frontal; *Fp*, pineal foramen; *JF*, interfrontal; *P*, parietal; *PP*, postparietal; *Ps*, parasphenoid; *Se*, ethmoid; *So*, supraoccipital. Reduced (modified after Broom). See also Watson, Phil. Trans. Roy. Soc., vol. 209 B, p. 23, fig. 11.

Ganoids, and the union of the two rami in front seems to have been usually ligamentous. The dentary bone (*d*) forms the greater part of the mandibular symphysis, and extends along the oral border of the ramus bearing the teeth. Below and within the anterior portion of the dentary is the comparatively small splenial (*s* and *sp*), which also enters the symphysis and is followed behind by a postsplenial (or preangular) (*ps*). Then, on the outer face and lower border, there is the large angular (*ag*), which extends to the stout articular (*ar*). The latter bone bears a deep, transversely extended facet for articulation with the quadrate of the upper jaw. On the inner face there is a large prearticular (or goniale) (*par*), and along the upper border there may be separate bones known as coronoid (*c*), intercoronoid (*ic*), and procoronoid (*prc*). The teeth are in regular series, decreasing in size posteriorly; though sometimes one or two greatly enlarged teeth occur at the symphysis.

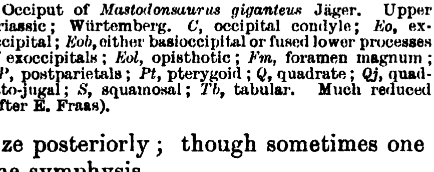


FIG. 289.

Occiput of *Mastodonsaurus giganteus* Jäger. Upper Triassic; Würtemberg. *C*, occipital condyle; *Eo*, exoccipital; *Eob*, either basioccipital or fused lower processes of exoccipitals; *Eol*, opisthotic; *Fm*, foramen magnum; *PP*, postparietals; *Pt*, pterygoid; *Q*, quadrate; *Qj*, quadrato-jugal; *S*, squamosal; *Tb*, tabular. Much reduced (after E. Fraas).

The *teeth*[1] of the smaller Palaeozoic Stegocephalians are smooth, slender, hollow, and conical (Figs. 294, *A*, *B*), and implanted either directly in the supporting bone, or attached by a cement base. Very often the lower half or two-thirds of the crown is externally grooved or striated, in which case a radial infolding of the dentine extends for an equal height (Fig. 295, *B*). Numerous fine dentine tubules extend downward toward the periphery, and tangentially to the walls of the radial prolongations of the pulp cavity. In the

[1] *Credner, H.*, Zur Histologie der Faltenzähne paläozoischer Stegocephalen. Abhandl. k. sächs. Ges. Wiss., math.-phys. Cl., vol. xx., p. 477, 1893.

more complicated teeth, secondary and even tertiary branching of dentine tubules may occur, and at the same time undulating or tortuously folded layers of cement, such as covers the exterior of the tooth, may become intercalated between the bundles of dentine tubules. This gives rise to the highly characteristic *labyrinthodont* structure, which reaches its extreme develop-

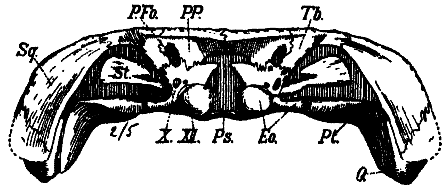


FIG. 290.
Occiput of *Batrachosuchus*. Middle Triassic; South Africa. *Eo*, exoccipital; *PFo*, post-temporal fossa; *PP*, postparietal; *Ps*, parasphenoid; *Pt*, pterygoid; *Q*, quadrate; *Sq*, squamosal; *St*, stapes; *Tb*, tabular; *X*, *XII*, foramina for nerves. Much reduced (after Watson).

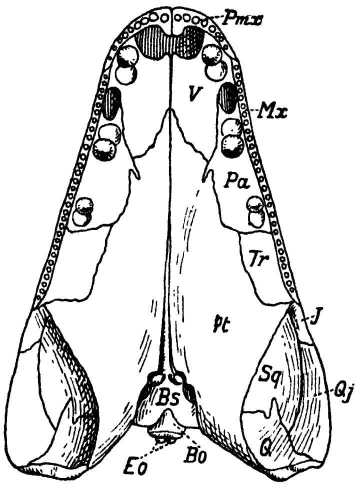


FIG. 291.
Palate of *Loxomma* (*Orthosaurus*). Coal Measures; England. *Bo*, basioccipital; *Bs*, basisphenoid; *Eo*, exoccipital; *J*, jugal; *Mx*, maxilla; *Pa*, palatine; *Pmx*, premaxilla; *Pt*, pterygoid; *Q*, quadrate; *Qj*, quadrato-jugal; *Sq*, squamosal; *Tr*, transverse (ectopterygoid); *V*, vomer. Nearly $1/4$ nat. size (after Watson).

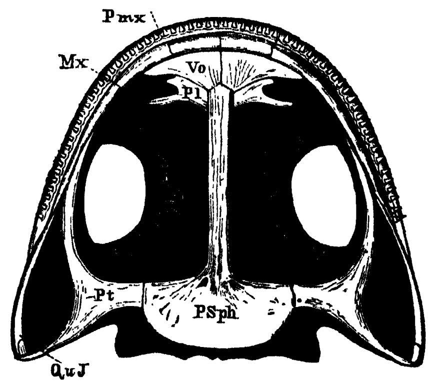


FIG. 292.
Palate of *Branchiosaurus*, restored by Credner. Lower Permian; Saxony. *Mx*, maxilla; *Pl*, palatine; *Pmx*, premaxilla; *PSph*, parasphenoid; *Pt*, pterygoid; *QuJ*, quadrato-jugal; *Vo*, vomer. Twice nat. size.

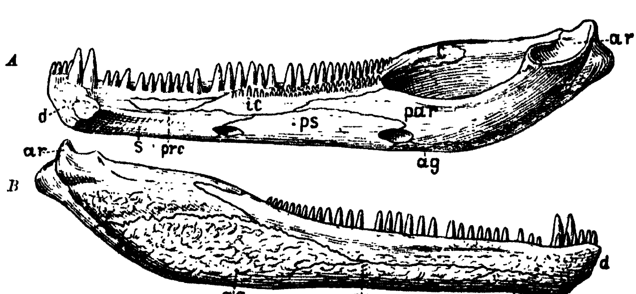


FIG. 293.
Lower jaw of *Trimerorhachis*, inner (*A*) and outer (*B*) view. Permian; Texas. *ag*, angular; *ar*, articular; *c*, coronoid; *d*, dentary; *ic*, intercoronoid; *par*, prearticular or goniale; *prc*, procoronoid; *ps*, postsplenial or preangular; *s*, *sp*, splenial. Much reduced (after Williston).

ment among the larger and geologically later Stegocephalians (Fig. 296), and almost or completely obliterates the pulp cavity. The internal structure becomes progressively less complicated toward the apex of the tooth; and above

the zone where radial infoldings of the wall leave off, the dentine is traversed simply by straight tubules radiating from the pulp cavity. The insertion of the teeth may be of the acrodont or pleurodont type, as already described, or they may be seated in shallow alveoli.

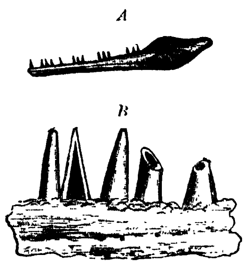


FIG. 294.
Lower jaw of *Branchiosaurus* with simple, smooth teeth. *A*, 1/1. *B*, enlarged (after Credner).

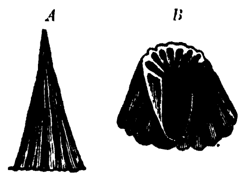


FIG. 295.
Tooth of *Archegosaurus*, enlarged. *A*, outer surface. *B*, lower half with a portion broken away to show the folded dentine.

Traces of branchial arches are conspicuous in the young of several Palaeozoic genera, and they are so close to the middle line that they doubtless supported internal gills. The arches persisted throughout life in the Permian *Dvinosaurus*, and in this genus they are so widely separated from the median line that they must have supported permanent large external gills as in many existing *Urodela*.

The Stegocephalian *pectoral arch* (Figs. 297, 298) is of unique construction, differing from that of other Amphibians in notable respects. The most characteristic, as well as the largest and usually best preserved bones, occupy an external position on

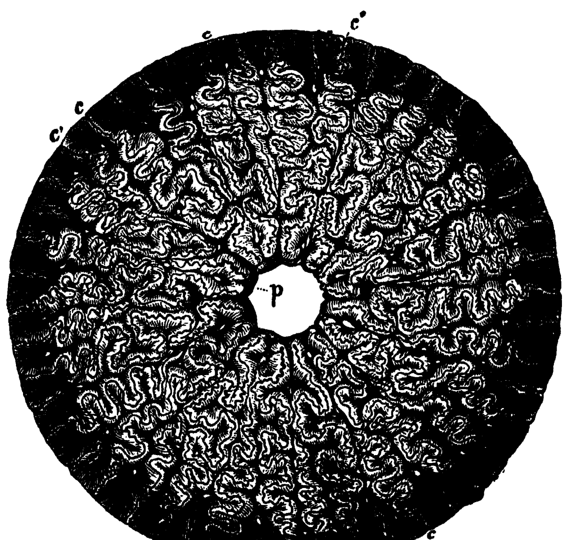


FIG. 296.
Transverse section of tooth of *Mastodonsaurus*. Upper Triassic; Würtemberg. *c*, *c'*, cement; *p*, pulp cavity. Three times nat. size (after Owen).

the thorax between the pectoral limbs. These bones are three in number, and as a rule prominently sculptured. The median element, identified as the interclavicle (episternum or entosternum), varies considerably in form and size among different genera. Most frequently it is rhombic, but sometimes transversely oval, and it may terminate behind in a long median extension.

Partly overlapping the forward portion of the interclavicle are the paired

plates which correspond to the clavicles of other Amphibians. Their posterior end is slender and slightly curved upwards; the anterior end is usually

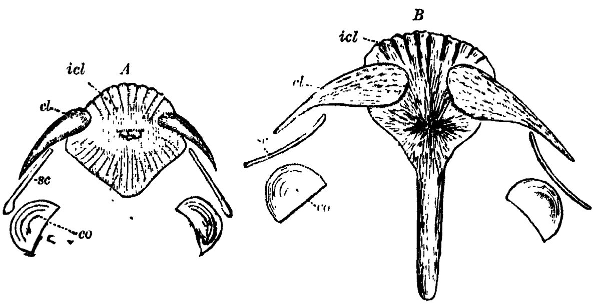


Fig. 297.

A, Pectoral arch of *Branchiosaurus*. *B*, *Melanerpeton*. *cl*, clavicle; *co*, coracoid; *icl*, interclavicle; *sc*, cleithrum. Magnified (after Credner).

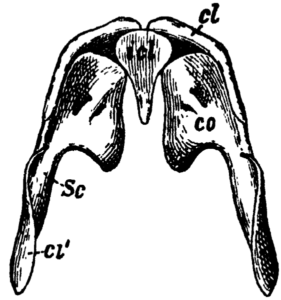


Fig. 298.

Pectoral arch of *Cacops aspidephorus* Williston, dorsal view. Permian; Texas. *cl*, clavicle; *cl'*, cleithrum; *co*, coracoid; *icl*, interclavicle; *sc*, scapula. 1/3 nat. size (after Williston).

expanded into a triangular or oval plate, often sculptured, but sometimes smooth as if it had been embedded in the integument. Adjacent to the posterior or distal end of the clavicle there is a narrow or rod-like piece with expanded distal end, which is evidently the cleithrum. The scapula and coracoid are often incompletely ossified and scarcely seen in the fossils; sometimes, however, they are not only ossified but fused together into a single piece.

The bones of the limbs, so far as known, agree in form, number, and arrangement with those of living Urodeles. The humerus is rarely furnished with articular condyles, its extremities remaining as a rule cartilaginous. Ulna and radius are always separate, simple, more or less elongate, and without articular facets. The carpus is imperfectly known; in many Palaeozoic genera it appears to have been cartilaginous, in others partly ossified. The metacarpals and phalanges are slender and elongate, and there are usually only four digits.

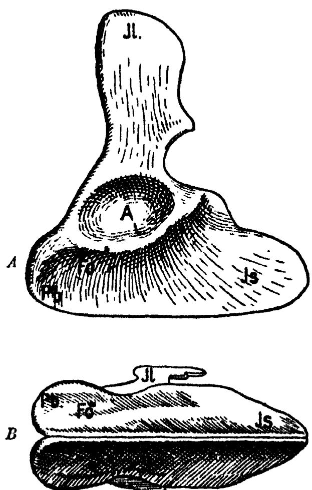


Fig. 299.

Pelvis of *Eryops megacephalus* Cope, left outer view (*A*) and from below (*B*). Permian; Texas. *A*, acetabulum for femur; *Fo*, obturator foramen; *Jl*, ilium; *Js*, Ischium; *Pb*, pubis. Much reduced (after Broili).

The *pelvic arch* (Fig. 299) is strongly developed, but seldom well preserved. The ilium (*Jl*) is short, stout, somewhat expanded at the extremities, and attached to a sacral rib. Ischium (*Js*) and pubis (*Pb*) sometimes unite to form a single large plate (ischio-pubis), pierced by an obturator foramen (*Fo*), or they may remain separate. The inner edges of the ischia form a symphysis in the median line. The pubes, which are smaller, sometimes remain cartilaginous.

The *hind limb* (Fig. 300) is almost always more strongly developed than the fore limb. The femur is a strong, elongate bone, without an ossified

capitulum, but often with well-formed distal condyles. Tibia and fibula remain separate, and resemble the corresponding bones of the anterior limb. The tarsus is either cartilaginous or composed of two rows of small bones, with centralia between. The pes is provided with five digits, but is otherwise closely similar to the manus; sometimes the second digit is the longest, in other cases the third.

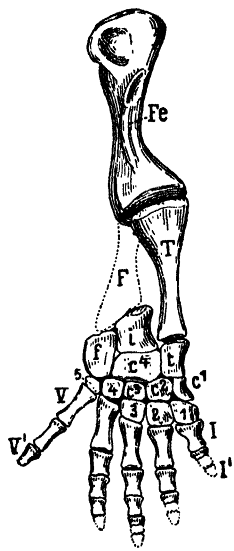


Fig. 300.

Left hind limb of *Trematops milleri* Williston, hinder view. Permian; Texas. C^{1-4}, centralia; *F*, fibula; *f*, fibulare; *Fe*, femur; *i*, intermedium; *T*, tibia; *t*, tibiale; *I-V*, metatarsals; I^1-V^1, phalanges. Much reduced (after Williston).

It has sometimes been assumed[1] that certain coprolites bearing the mark of a spiral valve, which are found with the *Stegocephali* in Permian formations, belong to these primitive Amphibians. There is, however, no proof hitherto of the correctness of this assumption, and the coprolites in question are probably referable to the associated Elasmobranch and Dipnoan Fishes.

The mode of occurrence of Stegocephalians in the Coal Measures, Lower Permian, and Keuper, indicates that they usually lived either in fresh water or on land. A few forms, however, found abundantly in marine Triassic deposits in Spitzbergen, may have existed in the open sea. Some of the smaller species appear to have taken refuge or fallen into hollow tree-stumps, since in Nova Scotia, at least, their remains are commonly found in cavities of decayed Sigillarian and Lepidodendroid trunks.[2] The larger forms, some of which attained gigantic size, were predatory, and probably subsisted on other amphibians, fishes, and crustaceans. From the shape of the skull and the relative size of the paired limbs, it may be inferred that the known Carboniferous and Permian groups were mainly dwellers in swamps or even in part terrestrial, the Triassic groups mainly aquatic. The largest species are Upper Triassic.

As originally pointed out by Cope, the temnospondylous *Stegocephali* are so closely similar to the *Cotylosauria* (p. 240) that they may be regarded as the direct ancestors of the *Reptilia*. According to D. M. S. Watson, the evolution of some of these *Stegocephali* is also in the direction of the modern *Amphibia*. The acquisition of a double occipital condyle, the gradual enlargement of the interpterygoid vacuities in the palate, and the ultimate articulation of the hinder part of the pterygoids with the parasphenoid, are all characters approaching those of the existing *Urodela* and *Anura*.

Sub-Order I. TEMNOSPONDYLI.[3]

Notochord more or less persistent. Vertebrae usually composed of several pieces, sometimes embolomerous, sometimes rhachitomous; in later types stereospondylous.

[1] *Neumayer, L.*, Die Koprolithen des Perms. Palaeontographica, vol. li., p. 121, 1904.—*Woodward, A. S.*, The so-called Coprolites of Ichthyosaurians and Labyrinthodonts. Geol. Mag. [6], vol. iv., p. 540, 1917.

[2] *Dawson, J. W.*, Recent Explorations of the erect Trees containing Animal Remains in the Coal Formation of Nova Scotia. Phil. Trans. Roy. Soc., vol. 173, p. 621, 1882.

[3] *Broom, R.*, Permian Temnospondylous Stegocephalians of North America. Bull. Amer. Mus. Nat. Hist., vol. xxxii., p. 563, 1913.—*Moodie, R. L.*, The Temnospondylous Amphibia

Basioccipital region and carpus and tarsus usually ossified. Teeth with radially infolded walls.

A. EMBOLOMERI.[1]

Basioccipital and basisphenoid ossified; occipital condyle concave, single or triple. Supraoccipital usually ossified. Pterygoids movably articulating with facet on basipterygoid processes of basisphenoid, expanded and meeting in symphysis in front; interpterygoid vacuities very small. Tabular and postparietal bones usually without occipital flanges. Vertebrae embolomerous. Ribs double-headed.

Family 1. **Anthracosauridae.**[2]

Occipital condyle single or triple. Tabular bone with a posterior process, which may support the pectoral arch. No post-temporal fossae. Clavicles are flat plates with parallel anterior and posterior margins. Carboniferous and Lower Permian.

Anthracosaurus Huxley. Skull somewhat longer than broad, with bluntly rounded snout. Orbits small and close together in middle of skull. Teeth round or ovoid in section, with fine vertical striations at the base and compressed to two sharp edges at the apex; large tusks on the transverse (ectopterygoid) and palatine bones. Vomer toothless. *A. russelli* Huxley, with skull nearly 40 cm. long. Upper Carboniferous (Lower Coal Measures); Airdrie, Lanarkshire.

Pteroplax Hancock and Atthey. Coal Measures; Northumberland.

Otocratia Watson. Otic notch closed behind, becoming foramen. Lower Carboniferous; Burdiehouse, Midlothian.

Palaeogyrinus Watson. Coal Measures; Fifeshire.

Eogyrinus Watson. Coal Measures; Northumberland and Staffordshire.

Pholiderpeton Huxley. Coal Measures; Yorkshire.

Diplovertebron Fritsch (*Gephyrostegus* Jaekel) (Fig. 282). Roof of skull thin above the temporal region. Five digits in manus, with 2, 3, 3, 3, 4 phalanges. Sclerotic plates conspicuous. Pubis probably not ossified. Lower Permian (Gas-coal); Nürschan, Bohemia.

? *Nummulosaurus* Fritsch. L. Permian; Bohemia.

Eobaphetes Moodie (*Erpetosuchus* Moodie *nec* Newton). Coal Measures; Kansas, U.S.A.

and a new species of *Eryops* from the Permian of Oklahoma. Kansas Univ. Sci. Bull., vol. v., p. 235, 1911.—*Watson, D. M. S.*, The "Orders" Rachitomi and Stereospondyli. Phil. Trans. Roy. Soc., vol. 209B, no. 360, 1919.

[1] *Barkas, T. P.*, Illustrated Guide to the Fish, Amphibian, etc., Remains of the Northumberland Carboniferous Strata. London, 1873.—*Watson, D. M. S.*, The Evolution and Origin of the Amphibia. Phil. Trans. Roy. Soc., vol. 214B, no. 416, 1926.—The larger Coal Measure Amphibia. Mem. and Proc. Manchester Lit. and Phil. Soc., vol. lvii., no. 1, 1912.

[2] *Atthey, T.*, *Anthracosaurus russelli* Huxley. Ann. Mag. Nat. Hist. [4], vol. xviii., p. 146, 1876.—*Pteroplax cornuta* H. and A. *Loc. cit.*, vol. xx., p. 369, 1878.—*Hancock, A.*, and *Atthey, T.*, Notes on the Remains of some Reptiles and Fishes from the Shales of the Northumberland Coal Field. Ann. Mag. Nat. Hist. [4], vol. i., p. 266, 1868.—Mandibular Ramus of *Anthracosaurus russelli*. *Loc. cit.*, vol. vii., p. 73, 1871.—*Huxley, T. H.*, *Anthracosaurus russelli*, a new Labyrinthodont from the Lanarkshire Coal-field. Quart. Journ. Geol. Soc., vol. xix., p. 56, 1863.—New Labyrinthodont from Bradford [*Pholiderpeton scutigerum*]. *Loc. cit.*, vol. xxv., p. 309, 1869.—*Jaekel O.*, *Gephyrostegus bohemicus*. Zeitschr. Deutsch. Geol. Ges., vol. liv., p. 127 1902.

? *Ichthyerpeton* Huxley. Coal Measures; Kilkenny, Ireland.
? *Crassigyrinus* Watson. Lower Carboniferous; Midlothian.

Family 2. **Loxommidae.**[1]

Occipital condyle triple; tabular bone with small posterior process; large post-temporal fossae. Orbit extended as vacuity forwards. Carboniferous and Lower Permian.

Loxomma Huxley (*Mioganodus* Owen; *Orthosaurus, Megalocephalus* Barkas) (Figs. 283, 291, 301). Skull somewhat longer than broad, with rounded snout. Orbits far back. Teeth much laterally compressed to two sharp edges, but with round tumid base, which is coarsely fluted; large tusks on the vomer, palatine, and transverse (ectopterygoid) bones. *L. allmani* Huxley, from Lower Carboniferous, Gilmerton, near Edinburgh. *L. acutirhinus* Watson, from Upper Carboniferous (Lower Coal Measures), Airdrie, Lanarkshire. *L. pachycephalus* Barkas sp., with skull 30 cm. in length, from English Coal Measures, considered by Watson to differ generically from *Loxomma* in the absence of an intertemporal bone and the presence of an anterior palatal vacuity. ? *L. bohemicum* Fritsch, from Lower Permian, Nürschan, Bohemia; and fragments from Coal Measures, Linton, Ohio.

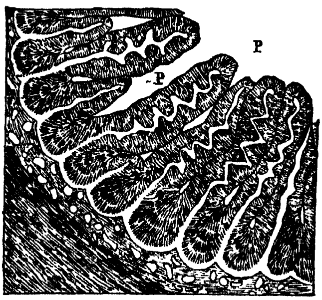


FIG. 301.

Cross-section of tooth of *Loxomma* (*Orthosaurus*), near the base. Enlarged. Coal Measures; Northumberland (after Embleton and Atthey). *P*, pulp cavity.

Baphetes Owen. Coal Measures; Nova Scotia, and perhaps Fifeshire and Lanarkshire, Scotland.
Macrerpeton Moodie. Coal Measures; Linton, Ohio.
Spathicephalus Watson. Lower Carboniferous; Midlothian.

Family 3. **Pholidogasteridae.**[2]

Vertebrae partly rhachitomous. Clavicles with triangular expansion on ventral surface. Lower Carboniferous.

Pholidogaster Huxley. Trunk very long and slender, with small feeble limbs. Pectoral arch apparently far back. Strong ventral armour of scutes. *P. pisciformis* Huxley, more than a metre long, from the ironstone of Gilmerton, near Edinburgh.

Family 4. **Cricotidae.**[3]

Snout much elongated; large oval orbits in hinder half of skull. Tabular bone with a posterior process, which may support the pectoral arch. Clavicles with

[1] *Embleton, D.*, and *Atthey, T.*, Skull and other bones of *Loxomma*. Ann. Mag. Nat. Hist. [4], vol. xiv., p. 38, 1874.—*Huxley, T. H.*, A new and large Labyrinthodont (*Loxomma allmanni* Huxley) in the Gilmerton Ironstone. Quart. Journ. Geol. Soc., vol. xviii., p. 291, 1862.—*Owen, R.*, Fossil imbedded in a mass of Pictou Coal from Nova Scotia [*Baphetes planiceps*]. Quart. Journ. Geol. Soc., vol. x., p. 207, 1854.

[2] *Huxley, T. H.*, *Pholidogaster pisciformis* Huxley. Quart. Journ. Geol. Soc., vol. xviii., p. 294, 1862.—*Watson, D. M. S.*, Palaeont. Hungarica, vol. i., p. 230, 1930 (wrongly dated 1926).

[3] *Case, E. C.*, Carnegie Inst. Washington, Publ. 146, p. 78, 1911, and Publ. 207, p. 158, 1915; Science, n.s., vol. xlii., p. 797, 1915.

triangular expansion on ventral surface. Lower Permian and probably Upper Carboniferous.

Cricotus Cope. Head bones feebly sculptured, sensory canals well marked. Teeth of unequal size. Ventral scutes rhomboidal. *C. heteroclitus* Cope. Lower Permian; Texas, U.S.A. Species also in L. Permian of Illinois and Kansas.

Cricotillus Case. Lower Permian; Oklahoma, U.S.A.

? *Spondylerpeton* Moodie. Coal Measures; Mazon Creek, Illinois.

? *Macromerion* Fritsch. Lower Permian; Bohemia.

? *Leptophractus* Cope. Coal Measures; Linton, Ohio.

Family 5. **Seymouriidae.**[1]

Skull triangular, with large oval orbits in hinder half. Occipital condyle single. Tabular and postparietal bones with occipital flanges. Pleurocentra relatively small. Clavicles expanded on ventral surface. Permian.

This family has usually been assigned to the Cotylosaurian Reptiles, but it is referred to the *Stegocephali* by Broom and also by Sushkin, who describes

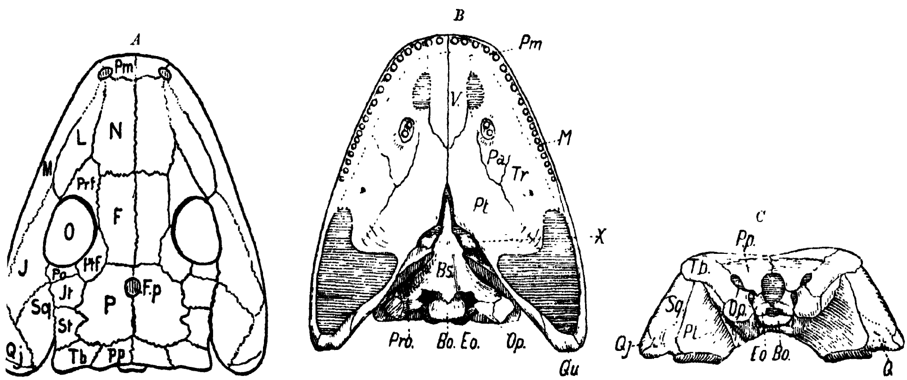


FIG. 302.

Seymouria baylorensis Broili. Skull from above (*A*), below (*B*), and in occipital view (*C*). Lower Permian; Texas. *Bo*, basioccipital; *Bs*, basisphenoid; *Eo*, exoccipital; *F*, frontal; *Fp*, pineal foramen; *Jt*, intertemporal; *J*, jugal; *L*, lachrymal; *M*, maxilla; *N*, nasal; *O*, orbit; *Op*, opisthotic; *P*, parietal; *Pa*, palatine; *Pm*, premaxilla; *Po*, postorbital; *Pp*, postparietal; *Prf*, prefrontal; *Pro*, prootic; *Pt*, pterygoid; *Ptf*, postfrontal; *Q*, quadrate; *Qj*, quadrato-jugal; *Sq*, squamosal; *St*, supratemporal; *Tb*, tabular; *Tr*, transverse (ectopterygoid); *V*, vomer; *X*, doubtfully separate basipterygoid process. $^1/_3$ nat. size. *A* after Broili; *B*, *C* after Watson.

the stapes as not abutting on the quadrate but tapering distally with a facet towards the otic notch for connection with the tympanic membrane. The teeth are labyrinthodont in structure, and the mandible is typically Stegocephalian.

Seymouria Broili (*Conodectes* Cope; *Desmospondylus* Williston) (Fig. 302).

[1] *Broili, F.*, Zahnbau von *Seymouria*. Anat. Anzeig., vol. 63., p. 185, 1927.—*Broom, R.*, Persistence of the Mesopterygoid in Reptilian Skulls. Proc. Zool. Soc., 1922, p. 455.—*Pearson, H. S.*, *Solenodonsaurus* Broili. Ann. Mag. Nat. Hist. [9], vol. xiv., p. 338, 1924.—*Romer, A. S.*, A Skeletal Model of the Primitive Reptile *Seymouria*. Journ. Geol., vol. xxxvi., p. 248, 1928.—*Sushkin, P. P.*, Representatives of the *Seymouriamorpha*. Occas. Papers Boston Soc. Nat. Hist., vol. v., p. 179, 1925. See also Palaeont. Zeitschr., vol. viii., p. 309, 1927.—*Watson, D. M. S.*, On *Seymouria*. Proc. Zool. Soc., 1918, p. 267.—*Williston, S. W.*, American Permian Vertebrates (Chicago, 1911), p. 48. See also Journ. Geol., vol. xix., p. 232, 1911.

Head and clavicular bones sculptured. Prootic bone reaching cranial roof, and ear cavity opening into brain cavity. Otic notches narrow and deep. Supraoccipital not ossified. Twenty-three presacral vertebrae, ribs double-headed, and spinous processes low. A single sacral vertebra. A separate coracoid. Rhomboidal interclavicle with hinder process; apparently no cleithra. No abdominal ribs or plates. Humerus with entepicondylar foramen. Carpus and tarsus incompletely known. Phalangeal formula, 2, 3, 4, 5, 3. *S. baylorensis* Broili (Fig. 302), with skull about 12 cm. long, from Lower Permian, Texas, U.S.A.

Kotlassia Amalitzky. Skull more depressed, with larger post-temporal fossae; pleurocentra smaller. Twenty-six presacral vertebrae, one sacral. *K. prima* Amalitzky, from Upper Permian, North Dwina, Russia.

Karpinskiosaurus Sushkin. Eighteen presacral vertebrae, two sacrals; neural spines thickened distally. Upper Permian; North Dwina, Russia.

Solenodonsaurus Broili. Lower Permian (Gas-coal); Bohemia.

B. RHACHITOMI.

Basioccipital and basisphenoid ossified; occipital condyle triple or double. Pterygoid articulating with both basisphenoid and parasphenoid. Interpterygoid vacuities of medium to large size. Tabular and postparietal bones with occipital flanges. Vertebrae rhachitomous.

Family 1. **Archegosauridae.**[1]

Skull elongated in adult, the comparatively small orbits far back. Occipital condyle triple, ossified only in adult. Pterygoids reaching the vomer. Pubis unossified. Dermal scales sparse, rounded, concentrically striated. Permian and Permo-Carboniferous.

Archegosaurus v. Meyer (Figs. 277, *E*; 284, 295, 303, 304). Skull in the young obtusely triangular, scarcely longer than broad, but becoming greatly elongated in the adult, with broad, anteriorly rounded snout. External bones radially sculptured, sensory canals feebly marked. Orbits situated in about the middle of the skull in the young, and in hinder portion in mature individuals; sclerotic ring of 20-23 plates. External nares elongate, far forwards. Postorbitals triangular, squamosals very large, lachrymals long and narrow, basioccipital region not ossified in young, palatal vacuities large. Parasphenoid toothless, pterygoids with minute teeth, vomer with one or two pairs of relatively large teeth, and maxillae, premaxillae, and palatines each with a single series of teeth. Dentine deeply and simply folded in lower half of the crown. Denticles of branchial arches observed in young individuals. In the caudal region stout chevron bones are attached to the hypocentra, and intercalated between these are two wedge-shaped pieces (Fig. 284).

[1] *Burmeister, H.*, Labyrinthodonten aus dem Saarbrücken Steinkohlengebirge. Berlin, 1850.—*Jaekel, O.*, Die Organisation von *Archegosaurus*. Zeitschr. Deutsch. Geol. Ges., vol. xlviii., p. 505, 1896 (reviewed by *G. Baur*, Amer. Nat., p. 975, 1897).—*Mehl, M. G.*, *Chenoprosopus milleri* gen. et sp. nov.; in Permo-Carboniferous Vertebrates from New Mexico. Publ. Carnegie Inst. Washington, no. 181, p. 11, 1913.—*Meyer, H. von*, Reptilien aus der Steinkohlenformation in Deutschland. Palaeontographica, vol. vi., p. 59, 1857. Published separately in Cassel, 1858.—*Whittard, W. F.*, Palate and Mandible of *Archegosaurus decheni* Goldfuss. Ann. Mag. Nat. Hist. [10], vol. i., p. 255, 1928.

The interclavicle is rhomboidal, about half as long as the skull, and radially sculptured. Clavicles triangular, with short posterior pedicle; coracoid and scapula ossified. Fore limb less strongly developed than the hind limb, and with four digits. Ventral armouring of small, overlapping, transversely elongated scales, keeled, and pointed at one end (Fig. 277, *E*).

In H. von Meyer's elaborate Monograph, published in 1858, no less than 271 examples of *A. decheni* v. Meyer, from the Lower Permian of Lebach, near Saarbrücken, are described, and 102 are figured. The remains, usually lacking the tail, occur here in siderite nodules; some individuals must have been 1·5 m. long. This or other species in Rothliegendes of Saxony. *A. ornatus* A. S. Woodw., from Permo-Carboniferous, Kashmir.

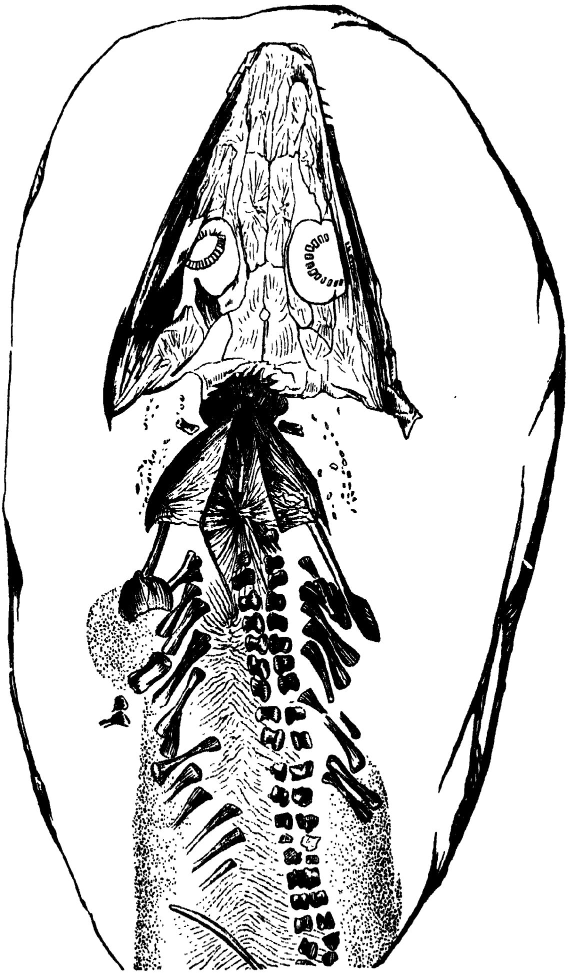


FIG. 303.

Archegosaurus decheni v. Meyer. Lower Permian; Lebach, near Saarbrücken. Young individual with traces of gill arches. 1/1 (after H. v. Meyer).

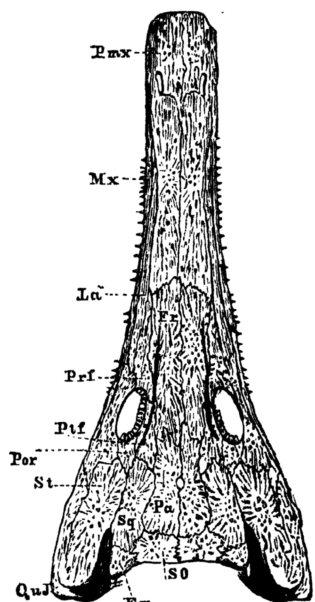


FIG. 304.

Archegosaurus decheni v. Meyer. Skull of adult individual, 1/2 nat. size. Lower Permian; Lebach, near Saarbrücken. *Ep*, tabular; *Fr*, frontal; *La*, lachrymal; *Mx*, maxilla; *Pa*, parietal; *Pmx*, premaxilla; *Por*, postorbital; *Prf*, prefrontal; *Ptf*, postfrontal; *QuJ*, quadrato-jugal; *SO*, postparietals; *Sq*, supratemporal; *St*, squamosal.

Chenoprosopus Mehl. Permo-Carboniferous; New Mexico, U.S.A.

Sparagmites Fritsch ; *Discosaurus* Credner (Fig. 277, *G*). Lower Permian ; Saxony and Bohemia.

Family 2. **Eryopidae.**[1]

As Archegosauridae, *but skull shorter and pubis ossified. Middle part of parasphenoid broad. Dermal scales more or less hexagonal and closely arranged.* Permian.

Eryops Cope (*Rhachitomus*, *Epicordylus*, *Parioxys*, *? Anisodexis* Cope) (Figs. 285, 288, 299, 305, 306). Largest of North American Stegocephalians.

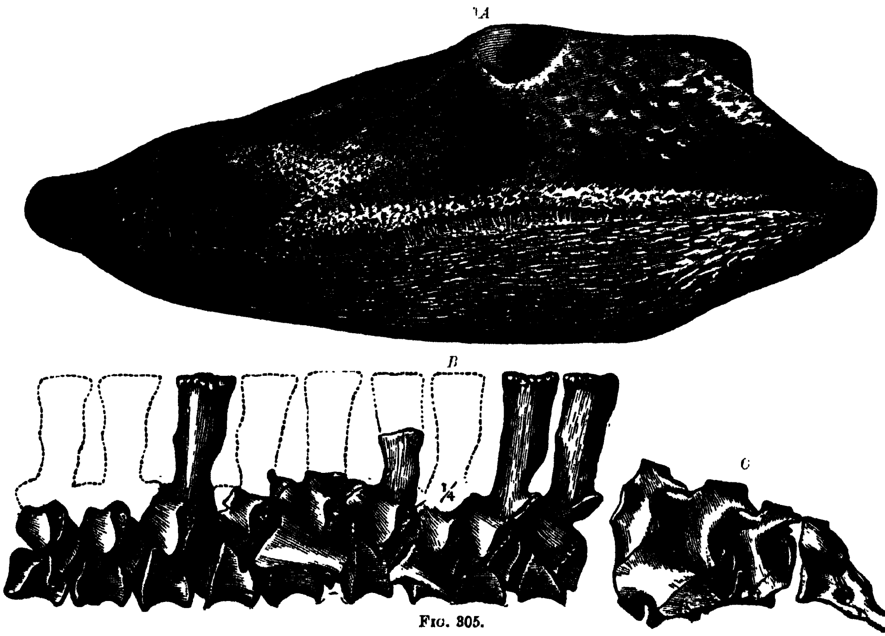


FIG. 305.

Eryops megacephalus Cope. Lower Permian ; Texas. *A*, Lateral aspect of skull. 1/5 nat. size. *B*, Portion of the vertebral column. *C*, Caudal vertebrae. 1/4 nat. size (after Cope).

Skull elongated triangular, with somewhat tapering snout. External nares large, widely separated. Cranial bones rugose, sutures indistinct. Parasphenoid very thick, dagger-shaped. On the palatine two large conical teeth. Maxilla and premaxilla with teeth of various sizes. Teeth sharply conical, at the tip smooth, at the base ribbed. Stout ribs with uncinate processes, those of the sacrum very broad and short. Caudal vertebrae few in number, those posteriorly

[1] *Branco, W.*, *Weissia bavarica*, nov. gen. et sp. Jahrb. k. preuss. geol. Landesanst., 1886, p. 22.—*Broili, F.*, *Eryops megacephalus* Cope. Palaeontographica, vol. xlvi., p. 61, 1899.—*Sclerocephalus* aus der Gaskohle. Jahrb. k. k. geol. Reichsanst. Wien, vol. lviii., p. 49, 1908 ; also Sitzb. bayer. Akad. Wiss., p. 199, 1926.—*Gaudry, A. L'Actinodon.* Nouv. Archives Mus. Hist. Nat. Paris, ser. 2, vol. x., p. 1, 1887.—*Huene, F. von*, Schädel von *Eryops*. Anat. Anzeig., vol. xli., p. 98, 1912.—*Miner, R. W.*, Pectoral Limb of *Eryops* and other Primitive Tetrapods. Bull. Amer. Mus. Nat. Hist., vol. li., p. 145, 1925.—*Wadia, D. N.*, and *Swinton, W. E.*, *Actinodon risinensis*, n. sp., in the Lower Gondwanas of Vihi District, Kashmir. Rec. Geol. Surv. India, vol. lxi., p. 141, 1928.—*Williston, S. W.*, *Eryops* Cope. Contrib. Walker Mus. Chicago, vol. ii., p. 87, 1918.

fused into a triangular piece tapering acutely behind. Fore and hind feet with five toes. *E. megacephalus* Cope, with skull 40-60 cm. long, and 30-46 cm. wide at occiput. Permian; Texas, Oklahoma, and New Mexico.

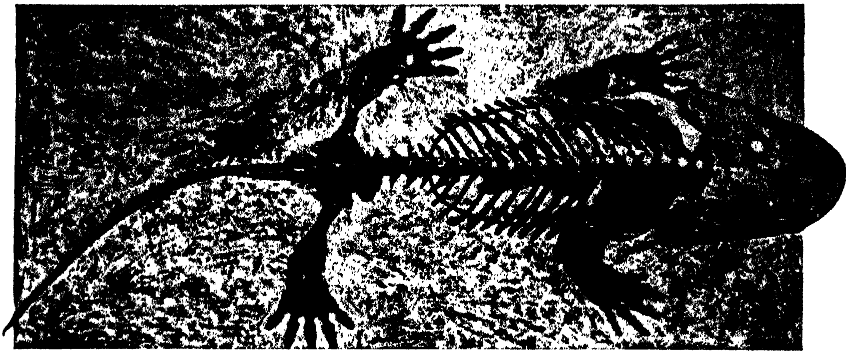


FIG. 306.
Eryops megacephalus Cope. Lower Permian; Texas. Mounted skeleton, much reduced (after Matthew).

Actinodon Gaudry (*Euchirosaurus* Gaudry) (Fig. 307). Vomers each with one large tooth and numerous rugosities. Lower Permian of Autun, France, and Rhenish Prussia; Permo-Carboniferous of Kashmir.

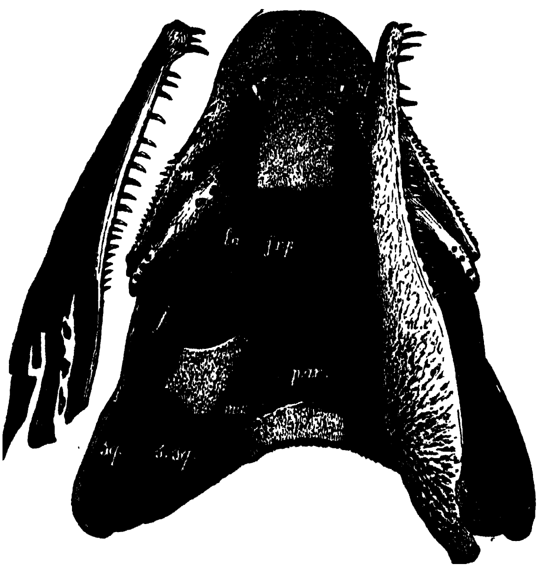


FIG. 307.
Actinodon frossardi Gaudry. Lower Permian; Muse, near Autun, France. Palatal aspect of skull, with rami of lower jaw. $^2/_5$ nat. size (after Gaudry).

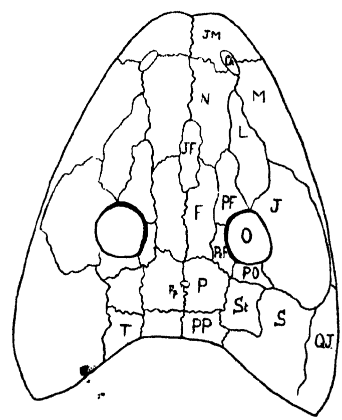


FIG. 308.
Osteophorus roemeri H. von Meyer. Roof of skull. Middle Rothliegendes; Silesia. *Ch*, external nostril; *F*, frontal; *Fp*, pineal foramen; *J*, jugal; *JF*, internasal; *JM*, premaxilla; *L*, lachrymal; *M*, maxilla; *N*, nasal; *O*, orbit; *P*, parietal; *PF*, prefrontal; *PO*, postorbital; *PP*, postparietal; *PtF*, postfrontal; *QJ*, quadrato-jugal; *S*, squamosal; *St*, supratemporal; *T*, tabular. About $^1/_5$ nat. size (after Frech).

Sclerocephalus Goldfuss (*Onchiodon* Geinitz; *Weissia* Branco) (Fig. 277, *F*). Over 1 m. long. Skull rounded anteriorly, orbits in hinder third, external nares far forwards, external bones coarsely sculptured. Palatines with

minute teeth, maxillae and premaxillae with a series of large, conical, vertically grooved teeth. Dentine deeply folded. Coracoid expanded, with concave posterior border; scapula long, slender, tapering. Phalangeal formula of hind foot, 2, 3, 4, 5, 4. Ventral scales oat-shaped. Lower Permian; Rhenish Prussia, Saxony, and Bohemia.

Melosaurus, *Chalcosaurus* H. v. Meyer; *Platyops* Trautschold. Permian; Russia.

Chelydosaurus Fritsch. Tabular bones pointed behind. Lower Permian; Braunau, Bohemia.

? *Osteophorus* H. von Meyer (Fig. 308). With a median internasal bone (*JF*). Lower Permian; Silesia.

Family 3. **Rhinesuchidae.**[1]

Small orbits far back. Pterygoids not reaching the vomer. Occipital condyle double. Pubis ossified. Upper Permian and Lower Triassic.

Rhinesuchus Broom. Palatine with numerous minute teeth, which are still smaller on the pterygoid and parasphenoid. *R.* ("*Eryops*") *africanus* Lydekker, *R. whaitsi* Broom, and other species. Lower and Middle Beaufort Beds; South Africa. *R. nyasaensis* Haughton. Karroo Formation; Nyasaland. *R. guembeli* v. Ammon sp. Permian; Rhenish Prussia. Also species in the Lower Triassic of Vologda, Russia, and in the Permian, S. Madagascar.

Uranocentrodon v. Hoepen (*Myriodon* v. Hoepen). Skull much depressed; palatine with one row of large teeth. Caudal pleurocentra double. Pelvis like that of *Eryops*. Carpus and tarsus incompletely ossified. *U. senekalensis* v. Hoepen, about 375 cm. in length. Beaufort Beds; Orange Free State, S. Africa.

Laccocephalus Watson. Upper Permian or Lower Trias; Orange Free State.

Laccosaurus Haughton. Lower Beaufort Beds; Cape Colony.

Benthosaurus Efremov. Upper Permian; N. Dwina, Russia.

Wetlugasaurus Riabinin. Lower Triassic; Wetluga River, N. Russia.

Gondwanasaurus Lydekker. Bijori, Central Provinces, India.

Family 4. **Zatrachysidae.**[2]

Skull depressed, small orbits far back. Large median anterior facial vacuity. Interpterygoid vacuities small. Permian.

The anterior vacuity in the cranial roof and the palate probably denotes the presence of a well-developed intermaxillary gland for producing the sticky

[1] *Broom, R.*, New Labyrinthodont *Rhinesuchus whaitsi*, from the Permian Beds of South Africa. Ann. S. African Mus., vol. iv., p. 373, 1908.—Temnospondylous Stegocephalian *Rhinesuchus*. Trans. Geol. Soc. S. Africa, vol. xiv., p. 79, 1912.—*Efremov, J.*, *Benthosaurus sushkini*, ein neuer Labyrinthodont der Permo-Triassischen Ablagerungen des Scharschengaflusses, Nord-Düna-Gouvernement. Bull. Acad. Sci. Leningrad, ser. vii., no. 8, 1929.—*Haughton, S. H.*, Genus *Rhinesuchus* Broom. Ann. S. African Mus., vol. xii., p. 65, 1915.—*Hoepen, E. C. N. van*, Stegocephalia of Senekal, O.F.S. Ann. Transvaal Mus., vol. v., p. 125, 1915.—*Riabinin, A. N.*, *Wetlugasaurus angustifrons* nov. gen. nov. sp. from the Lower Triassic of Vetluga-Land in Northern Russia. Proc. Russian Palaeontol. Soc., vol. viii., p. 49, 1930.—*Watson, D. M. S.*, Stegocephalia of Senekal, O.F.S. Geol. Mag., 1916, p. 83.

[2] *Huene, F. von*, Neubeschreibung des permischen Stegocephalen *Dasyceps bucklandi* (Lloyd). Geol. u. Palaeont. Abhandl., n.s., vol. viii., p. 325, 1910.

substance by which the prey adheres to the tongue. If so, the *Zatrachysidae* must have lived chiefly on land.

Zatrachys Cope. Palate with minute clustered teeth. Tabular bones somewhat produced behind. A pair of deep pits on the cranial roof between the orbits and the nostrils are supposed by Nopcsa to have been occupied by sensory tentacles like those of the existing Coecilians. Permian; Texas.

Platyhystrix Williston. With relatively long neural spines. Permian; New Mexico, U.S.A.

Dasyceps Lloyd. Permian; Kenilworth, England.

Family 5. **Trimerorhachidae.**[1]

Skull depressed, small orbits far forwards. Occipital condyle triple. Interpterygoid vacuities large. Pubis unossified. Permian.

Trimerorhachis Cope (Fig. 293). Pleurocentra very small, hypocentra delicate, and neural arches low. Skeleton imperfectly ossified, and ventral scales very thin. Permian; Texas and Oklahoma, U.S.A.

? *Tersomius* Case. Permian; Texas.

Family 6. **Lydekkerinidae.**[2]

Skull depressed, small orbits median. Double occipital condyle. Interpterygoid vacuities large. Pubis unossified. Lower Triassic.

Lydekkerina Broom. *L.* ("*Bothriceps*") *huxleyi* Lyd. Middle Beaufort Beds; Orange Free State, S. Africa.

Family 7. **Micropholidae.**[3]

Skull depressed, large orbits lateral and auditory (otic) notches lateral. Double occipital condyle. Interpterygoid vacuities large. Triassic.

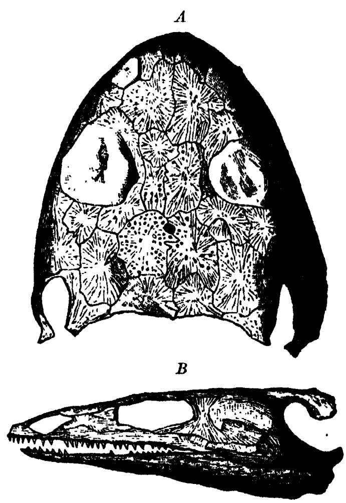


FIG. 309.
Micropholis granulata Owen sp. Trias; Table Mountain, South Africa. *A*, skull, from above; and *B*, in side view. Nat. size (after Owen).

Micropholis Huxley (*Petrophryne* Owen) (Fig. 309). No sensory canals, but a *ductus lachrymalis* in the large lachrymal bone. Small polygonal gular plates present. Cleithrum very slender. *M. stowi* Huxley. Upper Beaufort Beds; Cape Colony.

? *Rhinosaurus* Fischer de Waldheim. Russia.

[1] *Williston, S. W.*, *Trimerorhachis*, a Permian Temnospondyl Amphibian. Journ. Geol., vol. xxiii., p. 246, 1915. Also *Loc. cit.*, vol. xxiv., p. 291, 1916.

[2] *Broom, R.*, The Triassic Stegocephalians, *Brachyops*, *Bothriceps*, and *Lydekkerina*, gen. nov. Proc. Zool. Soc., 1915, p. 363.

[3] *Watson, D. M. S.*, *Micropholis stowi* Huxley, a Temnospondylous Amphibian from South Africa. Geol. Mag., 1913, p. 340.

Family 8. Cochleosauridae.[1]

Skull depressed, orbits median. Double occipital condyle. Interpterygoid vacuities small. Lower Permian.

Cochleosaurus Fritsch (*Melosaurus* Fritsch *nec* H. v. Meyer) (Fig. 287). Postparietals produced behind. Minute clustered teeth on the palate, and palatine bone with a few large teeth. *C. bohemicus* Fritsch, with skull sometimes 16 cm. long. Gas-coal; Nürschan, Bohemia.

Gaudrya, *Nyrania* Fritsch. Gas-coal; Nürschan, Bohemia.

? *Phrynosuchus* Broom. Lower Karroo Formation; S. Africa.

Family 9. Dvinosauridae.[2]

Skull depressed and broad, orbits forwards or median. No auditory (otic) notches. Interpterygoid vacuities large, and palate arched from side to side. Gills persistent throughout life. Some anterior vertebrae almost or completely stereospondylous. Permian.

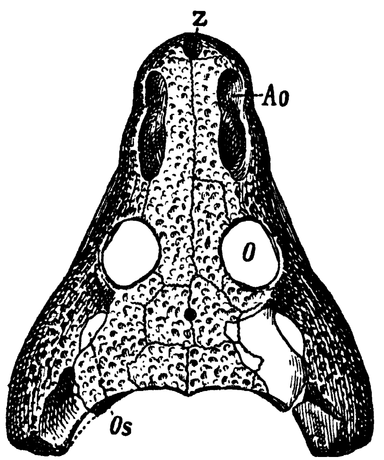


FIG. 310.

Trematops milleri Williston. Roof of skull. Permian; Texas. *Ao*, antorbital vacuity and nostril; *O*, orbit; *Os*, auditory notch surrounded by bone, falsely resembling a supratemporal vacuity; *Z*, anterior median vacuity. About 1/3 nat. size (after Williston).

Dvinosaurus Amalitzky. Pineal foramen almost or completely obliterated. Teeth with large pulp cavity. No ventral scutes. *D. primus* Amal. about 1 m. in length from Upper Permian, N. Dwina, Russia.

Family 10. Trematopsidae.[3]

Skull not depressed, orbits median. A pair of large antorbital vacuities continuous with the narial openings. Double occipital condyle. Pubis ossified. Permian.

Trematops Williston (Figs. 300, 310). Parasphenoid reduced. Palatines with two pairs of large teeth. Auditory (otic) notch closed behind to form a foramen. No conspicuous sensory canals. Ribs comparatively short. Permian; Clear Fork, Texas, U.S.A.

? *Acheloma* Cope. Permian; Texas.

Family 11. Dissorophidae.[4]

Skull short and not much depressed, large orbits median. No sensory canals. Auditory (otic) notches large, sometimes closed behind. Double occipital condyle.

[1] *Broili, F.*, *Cochleosaurus bohemicus* Fritsch. Palaeontographica, vol. lii., p. 1, 1905.—Ein Cotylosaurier aus der obercarbonischen Gaskohle von Nürschan in Böhmen. Sitzb. Bay. Akad. Wiss., math.-naturw. Abt., 1924, p. 3.

[2] *Amalitzky, W.*, The Dvinosauridae, a Family of Labyrinthodonts from the Permian of North Russia. Ann. Mag. Nat. Hist. [9], vol. xiii., p. 50, 1924. Notes also by *P. Sushkin* in Palaeont. Zeitschr., vol. viii., pp. 270-286, 1927.

[3] *Williston, S. W.*, *Trematops*, new genus. Journ. Geol., vol. xvii., p. 636, 1909.

[4] *Case, E. C.*, *Aspidosaurus glascocki* sp. nov. Bull. Amer. Mus. Nat. Hist., vol. xxviii., p. 179, 1910.—*Williston, S. W.*, *Dissorophus* Cope. Journ. Geol., vol. xviii., p. 526, 1910.—*Cacops, Desmospondylus.* Bull. Geol. Soc. America, vol. xxi., p. 249, 1910.—*Broiliellus*, a new genus. Journ. Geol., vol. xxii., p. 49, 1914.

A large cleithrum. Pubis ossified. A median or paired row of dermal bony plates along back. Permian.

Dissorophus Cope (*Otocoelus* Cope) (Fig. 286, *B*). Dorsal plates transversely elongated and covering greater part of body. Otic notch closed. *D. multicinctus* Cope. Permian; Clear Fork, Texas, U.S.A.

Cacops Williston (Fig. 298). Dorsal plates scarcely wider than vertebrae. Otic notch closed. Permian; Texas.

Aspidosaurus Broili (Fig. 278); *Alegeinosaurus* Case. Otic notch open behind. Permian; Texas.

Broiliellus Williston. Skull with low spines. Otic notch open behind. Permian; Texas and New Mexico.

? *Zygosaurus* Eichwald. Permian; Russia.

C. STEREOSPONDYLI.[1] (*Labyrinthodontia.*)

Basioccipital and basisphenoid much reduced, and a pair of exoccipital condyles. Interpterygoid vacuities very large. Pterygoids articulating with parasphenoid. Vertebrae completely ossified simple discs, slightly amphicoelous, sometimes centrally perforated for passage of the notochord. Teeth with complicated infolding of the dentine.

Family 1. Trematosauridae.[2]

Skull high, with lateral orbits and elongated slender snout. Parasphenoid very slender. Lower and Middle Triassic.

Trematosaurus Braun (Fig. 311). Skull elongated triangular, with orbits near the middle. Teeth present on jaw-bones, palatines, and vomer; and inner border of internal nares fringed with small denticles. A pair of greatly enlarged teeth present on symphysis of lower jaw, and behind these a supplementary row of small teeth. Two large vomerine tusks in advance of the internal nares,

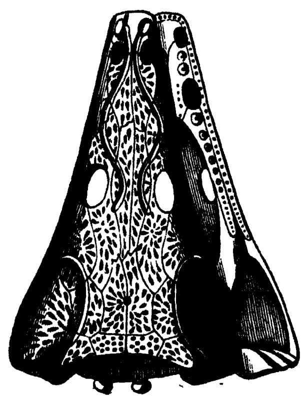


Fig. 311.

Skull of *Trematosaurus brauni* Burmeist. Bunter Sandstone; Bernburg. 1/4 nat. size (after Burmeister).

[1] *Fraas, E.*, Die Labyrinthodonten der schwäbischen Trias. Palaeontographica, vol. xxxvi., p. 1, 1889.—Neue Labyrinthodonten aus der schwäbischen Trias. *Loc. cit.*, vol. lx., p. 275, 1913. —*Huene, F. von*, *Gonioglyptus*, ein alttriassischer Stegocephale aus Indien. Acta Zoologica, vol. i., p. 433, 1920.—Organisation einiger Stegocephalen der schwäbischen Trias. *Loc. cit.*, vol. iii., p. 395, 1922.—*Schmidt, M.*, Labyrinthodonten und Reptilien aus den thüringischen Lettenkohlenschichten. Geol. u. Palaeont. Abhandl., n.f., vol. xviii., p. 231, 1931.—*Watson, D. M. S.*, "Orders" Rachitomi and Stereospondyli. Phil. Trans. Roy. Soc., vol. 209B, no. 360, 1919.—*Wepfer, E.*, Der Buntsandstein des Badischen Schwarzwalds und seine Labyrinthodonten. Berlin, 1923.—*Wills, L. J.*, Structure of Lower Jaw of Triassic Labyrinthodonts. Proc. Birmingham Nat. Hist. and Phil. Soc., vol. xiv., p. 1, 1916.—*Wiman, C.*, Stegocephalen aus der Trias Spitzbergens. Bull. Geol. Inst. Upsala, vol. xiii., p. 1, 1914.—Neue Stegocephalenfunde. *Loc. cit.*, vol. xiii., p. 209, 1916.—*Woodward, A. S.*, Two new Labyrinthodont Skulls of the genera *Capitosaurus* and *Aphaneramma*. Proc. Zool. Soc., vol. ii., p. 170, 1904.

[2] *Burmeister H.*, Die Labyrinthodonten aus dem bunten Sandstein von Bernburg. Berlin, 1840.—*Drevermann, F.*, Schädel von *Trematosaurus brauni*. Senckenbergiana, vol. ii., p. 83, 1920.—*Haughton, S. H.*, New Species of *Trematosaurus* (*T. sobeyi*). Ann. S. African Mus., vol. xii., p. 47, 1915.—*Seidlitz, W. von*, *Trematosaurus fuchsi*, etc. Palaeontographica, vol. lxiii., p. 87, 1920.

and three or four palatine teeth behind the same. Interclavicle rhomboid, with posterior pedicle. *T. brauni* Burm., with skull 25 cm. long, abundant in the Bunter Sandstone of Bernburg, N. Germany. Another species in M. Triassic, Kalmuck Steppe, Siberia.

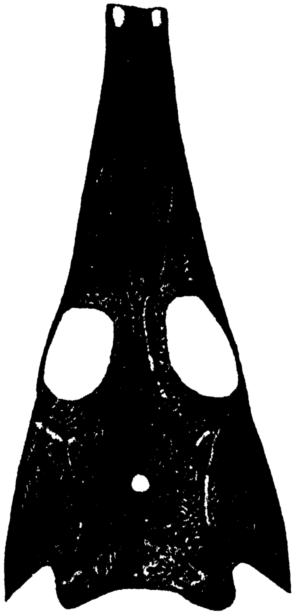


FIG. 312.
Lonchorhynchus öbergi Wiman. Roof of skull. Middle Triassic; Spitzbergen. 4/5 nat. size (after Wiman).

Trematosuchus Watson. *T. sobeyi* Haughton sp. Upper Beaufort Beds; S. Africa. *T. (?) yakovlevi* Riabinin. Triassic; Rybinsk, Russia.

Microposaurus Haughton. Upper Beaufort Beds; Wonderboom, S. Africa.

Gonioglyptus Huxley; *Glyptognathus* Lydekker. Triassic (Panchet Beds); India.

Aphaneramma A. S. Woodward; *Lonchorhynchus* Wiman (Fig. 312). Orbits large and snout much elongated. Middle Triassic; Spitzbergen.

Lyrocephalus Wiman. Snout relatively small; sensory canals very prominent. *L. euri* Wiman. Middle Triassic; Spitzbergen.

Tertrema Wiman. With closed otic notch. *T. acuta* Wiman. Middle Triassic; Spitzbergen.

Platystega Wiman. Middle Triassic; Spitzbergen.

Family 2. **Capitosauridae.**[1]

Skull longer than broad, and small orbits close together in hinder half. Parasphenoid slender. Triassic.

Capitosaurus Münster (*Parotosaurus* Jaekel) (Fig. 313). Snout broad and obtusely rounded. Orbits small. Nasals of equal size with the frontals or larger. A small auditory (otic) notch. One or two powerful tusks on vomer in front of the internal nares and on palatines behind the same. Between the vomer and premaxillae is a vacuity to receive the two median tusks of the lower jaw. *C. nasutus* Meyer (Fig. 313). Bunter; Bernburg, N. Germany. *C. helgolandiae* Schröder. Bunter; Heligoland. Other species in the European Muschelkalk. *C. bogdoanus* Sushkin. Middle Triassic; Kalmuck Steppe, Siberia. *C. africanus* Broom. Upper Beaufort Beds; S. Africa. *C. stantonensis* A. S. Woodward, from Lower Keuper, Staffordshire, intermediate between *Capitosaurus* and *Cyclotosaurus*.

Cyclotosaurus Fraas (Fig. 314). Similar to *Capitosaurus*, except that the auditory (otic) notch is closed behind by the union of the tabular bone with the squamosal. *C. robustus* Meyer sp. (Fig. 314). Keuper; Würtemberg. *C. spitzbergensis* Wiman. Middle Triassic; Spitzbergen. Another species in Hawkesbury Formation, New South Wales, Australia.

Kestrosaurus Haughton. Upper Beaufort Beds; Senekal, Orange Free State, S. Africa.

[1] ***Broili, F.***, ***Capitosaurus arenaceus*** **Münster. Centralbl. f. Min., etc., 1915, p. 569.—*Schroeder, H.*, Ein Stegocephalen-Schädel von Helgoland. Jahrb. k. preuss. geol. Landesanst., vol. xxxiii., p. 232, 1913.—*Swinton, W. E.*, New Species of *Capitosaurus* from the Trias of the Black Forest. Ann. Mag. Nat. Hist. [9], vol. xx., p. 177, 1927.**

Family 3. **Metoposauridae.**[1]

Skull low and broad, but elongated. Orbits in front half or median. Parasphenoid very broad. Triassic.

Metoposaurus Lydekker (*Metopias* v. Meyer) (Fig. 315). Skull large, broadly triangular, with elliptical orbits in anterior half, and large narial openings.

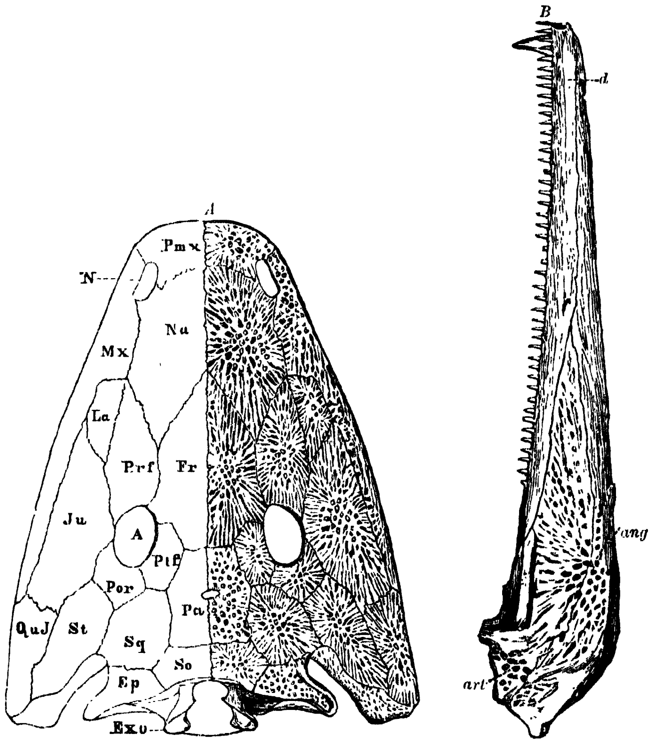


FIG. 318.

Capitosaurus nasutus H. von Meyer. Roof of skull (*A*) and right ramus of lower jaw (*B*). Bunter Sandstone; Bernburg. *Ep*, tabular; *So*, postparietal; *Sq*, supratemporal; *St*, squamosal. Other lettering as in previous figures.

Nasals shorter than frontals and parietals. Clavicular plates very large. Dentition weak, teeth strongly fluted externally, especially at the base, with but slight internal foldings. Ribs very powerful, distally expanded. *M. diagnosticus* v. Mey. Keuper; Würtemberg.

Trigonosternum M. Schmidt. Lettenkohle; Thuringia.

Buettneria Case. Parasphenoid narrower than in *Metoposaurus*. A row of small teeth on vomer at inner edge of internal narial opening. No posterior temporal fossae. *B. perfecta* Case, with skull 45 cm. long, from Upper Triassic, W. Texas.

Anaschisma Branson. Orbits small, in anterior half of skull. External

[1] *Branson, E. B.*, and *Mehl, M. G.*, Triassic Amphibians from the Rocky Mountain Region. Univ. Missouri Studies, vol. iv., no. 2, 1929.—*Case, E. C.*, New Species of *Buettneria*, with a Discussion of the Brain Case. Contrib. Mus. Paleont. Univ. Michigan, vol. iii., no. 11, 1931.

narial openings enlarged to receive median tusks of lower jaw. Auditory (otic) notches very small. *A. browni* Branson, with skull 50 cm. long, from Triassic, Lander, Wyoming. Other species perhaps in Arizona.

Koskinonodon, *Borborophagus* Branson and Mehl. Triassic; Wyoming. *Kalamoiketor* Branson and Mehl. Triassic; Arizona.

Dictyocephalus Leidy. Triassic; North Carolina.

? *Calamops* Sinclair. Triassic; Pennsylvania.

? *Peltostega* Wiman. Middle Triassic; Spitzbergen.

Family 4. **Mastodonsauridae.**

Skull low, longer than broad, with the large frontals entering the borders of the orbits, which are large, median, and close together. Parasphenoid slender. Triassic.

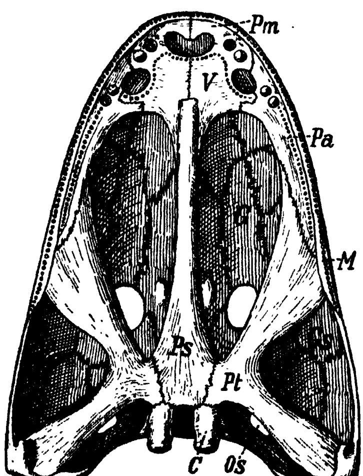


FIG. 314

Cyclotosaurus robustus H. von Meyer. Skull restored by E. Fraas, from below. Lower Keuper; Würtemberg. *C*, exoccipital condyle; *G*, interpterygoid vacuity; *Gs*, lateral palatal vacuity; *M*, maxilla; *Os*, auditory opening in cranial roof; *Pa*, palatine; *Pm*, premaxilla; *Ps*, parasphenoid; *Pt*, pterygoid; *V*, vomer. Much reduced (after E. Fraas).

FIG. 315.

Metoposaurus diagnosticus v. Meyer. Ventral aspect of skeletal fragment. Keuper; Hahnweiler, near Stuttgart. 1/8 nat. size (after E. Fraas).

Mastodonsaurus Jaeger (*Labyrinthodon* Owen) (Figs. 289, 296, 316). Largest of all Labyrinthodonts, skull 1·25 m. long, with the large orbits mainly behind the middle. External bones sculptured, sensory canals prominent. Premaxillae pierced for the passage of the two greatly enlarged teeth at symphysis of lower jaw. Vomers with a pair of tusks in front of the internal nares; palatines with another pair of tusks behind the nares and

a single series of large teeth. Dentine excessively complicated. Interclavicle rhomboidal, clavicles triangular, all strongly sculptured. Vertebral centra notched above where they form the base of the neural canal. Limbs imperfectly known, and dermal armour not observed. The finest specimens of *M. giganteus* Jaeger are from the Lettenkohle of Gaildorf and Oedendorf in Würtemberg. *M. acuminatus* E. Fraas from Lettenkohle of Würtemberg and Thuringia. Fragments occur also in the Upper Trias of England and India, and in the Bunter Sandstone of Alsace and the Black Forest.

Hercynosaurus Jaekel. Upper Keuper; Halberstadt.

Diadetognathus Miall. Keuper; Warwick.

Pachygonia Huxley. Triassic (Panchet Beds); India.

? *Mentosaurus* Röpke.[1] About as large as *Mastodonsaurus*. Lower Muschelkalk; near Halle.

? *Syphonodon* Seeley. Upper Karroo Formation; near Burghersdorp, S. Africa.

? *Ptychosphenodon* Seeley. Upper Karroo Formation; Aliwal North, S. Africa.

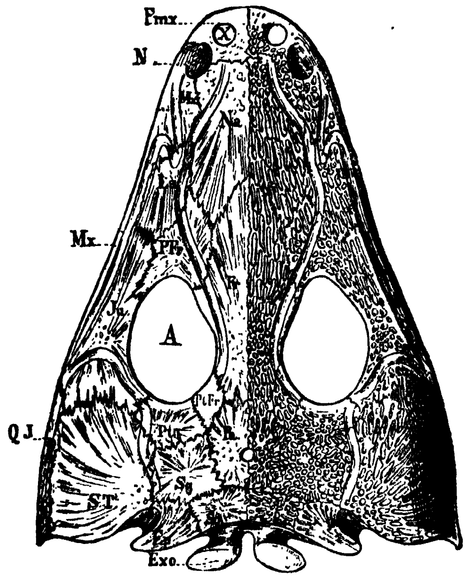


FIG. 316.

Skull of *Mastodonsaurus giganteus* Jaeger. Upper Keuper; Wurtemberg. *A*, orbit; *Ep*, tabular; *Exo*, exoccipital; *Fr*, frontal; *Ju*, jugal; *La*, lachrymal; *Mx*, maxilla; *N*, external nares; *Na*, nasal; *Pa*, parietal; *Pfr*, prefrontal; *Pmx*, premaxilla; *Ptfr*, postfrontal; *Pto*, postorbital; *Qj*, quadrato-jugal; *So*, postparietal; *Sq*, supratemporal; *ST*, squamosal; *X*, openings for the passage of the tusks of lower jaw. 1/16 nat. size (after E. Fraas).

Family 5. **Rhytidosteidae.**[2]

Skull depressed, broad and triangular, with narial openings and orbits lateral and laterally directed. Vomerine region relatively long. Upper Triassic.

Rhytidosteus Owen. Head bones with coarse radiate sculpture and slightly marked sensory canals. Palatal bones finely tuberculated. *R. capensis* Owen. Skull 25 cm. long, from Upper Karroo (Upper Beaufort Beds), Beersheba, Orange Free State.

Family 6. **Brachyopidae.**[3]

Skull depressed, very short and broad, with the large orbits far forwards. Palate arched from side to side. Triassic.

[1] *Röpke, W.*, *Mentosaurus Waltheri*, nov. gen. nov. sp. Leopoldina (Halle), vol. vi., p. 587, 1930.

[2] *Owen, R.*, A Labyrinthodont Amphibian (*Rhytidosteus capensis*) from the Trias of the Orange Free State. Quart. Journ. Geol. Soc., vol. xl., p. 333, 1884.

[3] *Broom, R.*, New Stegocephalian (*Batrachosuchus browni*) from the Karroo Beds of Aliwal North. Geol. Mag., 1903, p. 473.—*Huxley, T. H.*, *Bothriceps australis*. Quart. Journ. Geol. Soc., vol. xv., p. 642, 1859.—*Owen, R.*, Cranium of *Brachyops laticeps*. Quart. Journ. Geol. Soc., vol. xi., p. 37, 1855.—*Stephens, W. J.*, Labyrinthodont Fossils from the Hawkesbury Sandstone of New South Wales. Proc. Linn. Soc. N.S. Wales [2], vol. i., p. 1175, 1887; also *loc. cit.*, vol. ii., p. 156, 1888.—*Piveteau, J.*, [A Plagiosaurid from Upper Trias of Lunéville]. Ann. Paléont., vol. xvii., p. 23, 1928.

Brachyops Owen. Skull triangular and orbits widely separated; radiating ornament and lyra faint. *B. laticeps* Owen, skull 12 cm. wide, from Lower Gondwana formation, Mangali, Central India.

Bothriceps Huxley. Orbits closer together than in *Brachyops*, and ornament reticulated or pitted. *B. australis* Huxley, skull about 10 cm. wide, probably from Hawkesbury Formation, New South Wales. The immature *Platyceps wilkinsoni* Stephens, showing branchial arches, may be the young of *Bothriceps*.

FIG. 317.

Plagiosternum pulcherrimum E. Fraas. Skull, upper aspect. Lower Keuper; Pfaffenhofen, Würtemberg. *o*, orbit. 1/6 nat. size (after E. Fraas).

Batrachosuchus Broom (Fig. 290). Skull very broad and orbits widely separated; large narial openings nearly median in front; reticulated and radiating ornament and lyra strong. Karroo Formation; South Africa.

Plagiosternum E. Fraas (*Plagiosaurus* Jaekel) (Fig. 317). Skull very broad, orbits very large and close together; no auditory (otic) notches. Interclavicle much wider than long. In Germany ranging from Upper Muschelkalk to Middle Keuper. Perhaps includes *Xestorrhytias perrini* H. von Meyer, from the Muschelkalk of Lunéville.

Plagiosuchus v. Huene. U. Trias; Würtemberg, Thuringia, and Lorraine.

Fragments of Temnospondylous Stegocephalians are named as follows:—

Eupelor, *Pariostegus* Cope. Trias; N. America.

? *Eosaurus* Marsh. Amphicoelous vertebral centra. Upper Carboniferous; Nova Scotia.

Sub-Order 2. LEPOSPONDYLI. (*Microsauria* or *Holospondyli.*)

Vertebrae hourglass-shaped, but the constricted notochord passing through them; neural arch fused with centrum. Ribs long, curved, usually double-headed. Teeth simple, conical, hollow.

Except one generically indeterminable specimen from the Lower Carboniferous of Midlothian, described by Watson, all the remains of this Sub-Order have been found in the Upper Carboniferous and Lower Permian.

Family 1. Hylonomidae.

Lizard-like, usually long-tailed. Fore limbs less robust than the hinder pair; carpus and tarsus ossified or cartilaginous. Pubis ossified. Ventral, and in rare cases also the dorsal surface covered with small, round, oblong, oval or oat-shaped scales. Upper Carboniferous and Lower Permian.

Hylonomus Dawson (Figs. 277, *C*; 281, *A–C*; 318). Skull narrow, with smooth or faintly sculptured bones. Palatal teeth relatively small. Neural spines broad. Abdominal scales oval. *H. lyelli* Dawson (Fig. 318). Scattered remains in hollow tree stumps in Coal Measures, South Joggins, Nova Scotia.

Hyloplesion Fritsch. Cranial bones smooth, finely striated or punctate. Orbits large, with sclerotic ring. Tarsus ossified. According to Fritsch, both dorsal and ventral armature is present, composed of overlapping oval scales

with thickened posterior border. Lower Permian; Nürschan, Bohemia, and Niederhässlich, Saxony.

Hylerpeton Owen; *Smilerpeton*, *Fritschia* Dawson. Coal Measures; South Joggins, Nova Scotia.

Seeleya Fritsch. With rounded snout. Teeth on all bones of the palate, those of the premaxillae much larger than the maxillary teeth. Both dorsal and ventral armour present. Scales elongated oval, ornamented with undulating or dichotomising lines. Very rare in Lower Permian of Nürschan, Bohemia. *S. pusilla* Fritsch, less than 2·5 cm. in length.

Ricnodon[1], *Orthocosta*, *Microbrachis* Fritsch. Lower Permian; Nürschan, Bohemia.

Odonterpeton Moodie. Coal Measures; Linton, Ohio.

? *Petrobates* Credner (Fig. 277, *H*). Lower Permian; Saxony.

? *Limnerpeton* Fritsch. Lower Permian; Bohemia.

? *Dendrerpeton* Owen. Coal Measures; Nova Scotia.

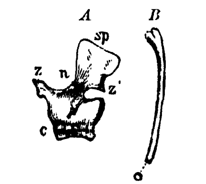


FIG. 318.

A, vertebra, and *B*, rib of *Hylonomus lyelli* Dawson. Coal Measures; South Joggins, Nova Scotia. *c*, centrum; *n*, neural canal; *sp*, neural spine; *z*, *z'*, zygapophyses.

Family 2. **Amphibamidae.**

Head relatively large and broad, trunk short and broad, and tail very short. Pubis of calcified cartilage. Carboniferous.

Amphibamus Cope. Skull with deep auditory (otic) notches. Coal Measures; Mazon Creek, Illinois. Considered by A. S. Romer to be a Branchiosaurian.

Cephalerpeton Moodie. Skull without auditory (otic) notches. Limbs unusually long. Coal Measures; Mazon Creek.

Family 3. **Urocordylidae.**[2] (*Nectridia* Miall.)

Stout and long-tailed. Postero-lateral angles of skull produced into cornua; orbits far forwards. Neural spines and chevrons of caudal vertebrae expanded distally and pectinated. Carpus and tarsus rarely ossified. Upper Carboniferous and Lower Permian.

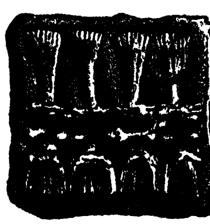


FIG. 319.

Urocordylus wandesfordi Huxley. Caudal vertebrae. Coal Measures; Kilkenny, Ireland. Nat. size (after Huxley).

Urocordylus Huxley (*Oestocephalus*, *Ctenerpeton* Cope) (Figs. 281, *F*; 319). Fore limb slightly less developed than the hind limb, both pentadactyle. Skull depressed, triangular, posteriorly truncate. Tail nearly twice as long as the trunk with the head, with about 80 vertebrae. Ventral armour of about 100 rows of scutes converging towards the median line, in form elongated oval, fusiform or oat-shaped. *U. wandesfordi* Huxl. Length about 50 cm. Coal Measures; Kilkenny, Ireland. *U. scalaris* Fritsch. Lower Permian; Nürschan, Bohemia. Other species in Coal Measures, Linton, Ohio.

[1] *Hummel, K.*, *Ricnodon* cf. *dispersus* Fritsch. Zeitschr. Deutsch. Geol. Ges., vol. 65., Abh. p. 591, 1913.

[2] *Andrews, C. W.*, *Keraterpeton galvani* Huxley, from Staffordshire. Geol. Mag., 1895, p. 81.—*Jaekel, O.*, *Ceraterpeton*, *Diceratosaurus*, and *Diplocaulus*. Neues Jahrb. f. Min., etc., 1903, vol. i., p. 109.—*Woodward, A. S.*, *Ceraterpeton galvani* Huxley. Geol. Mag., 1897, p. 293.

Lepterpeton Huxley (Fig. 320). Lizard-like, with narrow, elongated head and tapering snout. Hind limb slightly stouter than the fore limb. Ventral scales elongated rhombic. Coal Measures; Kilkenny, Ireland.

Keraterpeton (*Ceraterpeton*) Huxley. Length about 25 cm. Skull broad, rounded anteriorly, and external bones sculptured. Very small ventral scutes,

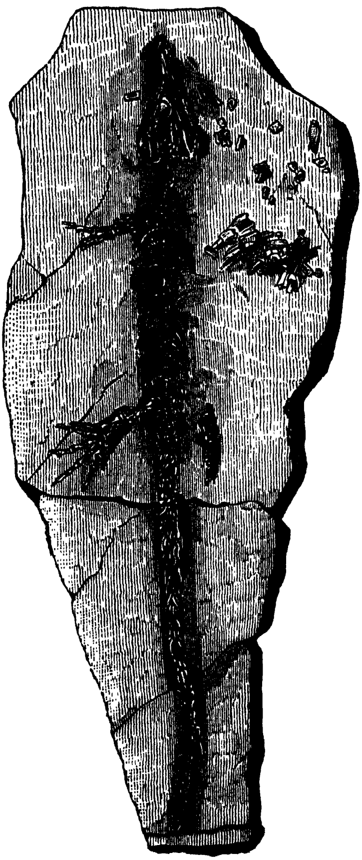


FIG. 320.
Lepterpeton dobbsi Huxley. Coal Measures; Kilkenny, Ireland. $^3/_4$ nat. size (after Huxley).

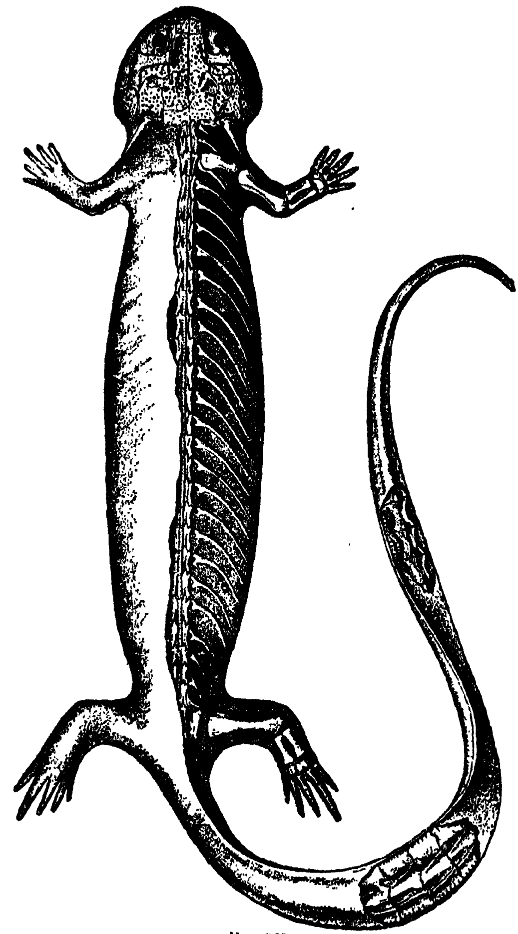


FIG. 321.
Scincosaurus crassus Fritsch. Lower Permian; Nürschan, Bohemia. Restored. Nat. size (after Fritsch).

and no dorsal armour. Phalangeal formula of hind foot, 2, 3, 4, 4, 3. Coal Measures; Kilkenny, Ireland, and Staffordshire, England.

Scincosaurus Fritsch (Fig. 321). Skull smaller in proportion to the body than in *Keraterpeton*, with more numerous presacral vertebrae, and distinct ossifications in carpus and tarsus. *S. crassus* Fritsch. Lower Permian; Bohemia.

Diceratosaurus Jaekel (*Eoserpeton* Moodie). With a small inner pair, and

large outer pair of cornua on the skull. *D. punctolineatus* Cope sp. Coal Measures; Linton, Ohio.

Sauropleura Cope (*Ptyonius*, *Hyphasma* Cope). Coal Measures; Linton, Ohio. Lower Permian Gas-coal; Bohemia.

Crossotelos Case. Lower Permian; Oklahoma, U.S.A.

Family 4. **Diplocaulidae.**[1]

Eyes far forwards, and postero-lateral angles of skull much produced both posteriorly and laterally. Ribs stout, double-headed. Tail as in Urocordylidae. *Cleithrum expanded at dorsal end,* T*-shaped in cross-section. Limbs very small.* Upper Carboniferous and Lower Permian.

Diplocaulus Cope (Figs. 281, *D*, *E*; 286, *A*; 322). Tadpole-shaped. Skull half-moon-shaped, much depressed, ornamented with pittings. Quadrate in the front half of the skull. The auditory (otic) notches very large and broad. Teeth small, uniform in size. The row of maxillary teeth extending for one-third to one-half the total length of the skull. A second row of teeth on the vomers and palatines, and in the symphysial part of the mandible. Neural arches fused with vertebral centra; zygosphene and zygantrum present; neural spines not ossified. A separate coracoid. Humerus with entepicondylar foramen. Front limbs smaller than the hind limbs. *D. magnicornis* Cope, nearly a metre in length, from Permian, Texas. Apparently other species in Upper Carboniferous, Illinois.

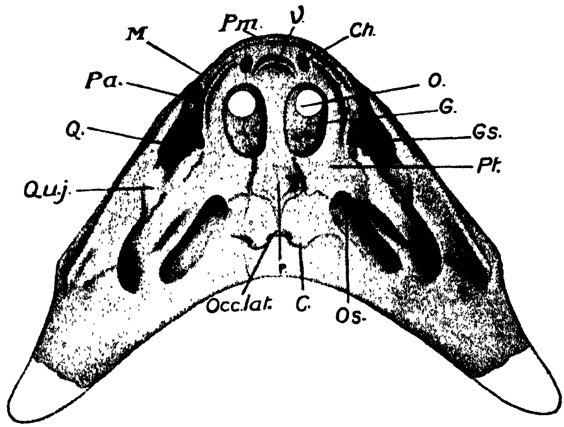


FIG. 322.

Diplocaulus magnicornis Cope. Skull, palatal aspect. Permian; Texas. *C*, exoccipital condyle; *Ch*, internal narial opening; *G*, interpterygoid vacuity; *Gs*, lateral palatal vacuity; *M*, maxilla; *O*, orbit; *Occ. lat.*, exoccipital; *Os*, closed auditory notch; *P*, parasphenoid; *Pa*, parietal; *Pm*, premaxilla; *Pt*, pterygoid; *Q*, quadrate; *Qu.j*, quadrato-jugal; *V*, vomerine region. About $^1/_5$ nat. size.

Batrachiderpeton Hancock and Atthey. Coal Measures; Northumberland.

Family 5. **Dolichosomidae.** (*Aistopoda* Miall.)

Body serpentiform, without either limbs or arches for their support. Ribs slender, single- or double-headed, with a kind of uncinate process. Upper Carboniferous and Lower Permian.

[1] *Broili, F.*, *Diplocaulus* Cope. Centralbl. f. Min., etc., 1902, p. 536.—*Douthitt, H.*, Structure and Relationships of *Diplocaulus*. Contrib. Walker Mus. Chicago, vol. ii., no. 1, 1917.—*Huene, F. von.*, Unterkiefer von *Diplocaulus*. Anat. Anzeig., vol. 42, p. 472, 1913.—*Moodie, R. L.*, Skull Structure of *Diplocaulus magnicornis* Cope. Journ. Morphology, vol. xxiii., p. 31, 1912.—*Watson, D. M. S.*, *Batrachiderpeton lineatum.* Proc. Zool. Soc. Lond., 1913, p. 949.—*Williston, S. W.*, Skull and Extremities of *Diplocaulus*. Trans. Kansas Acad. Sci., vol. xxii., p. 122, 1909.

Dolichosoma Huxley (? *Phlegethontia* Cope) (Fig. 323). Skull relatively small, triangular, with tapering snout; external bones smooth, and median bones more or less fused. Premaxillae very small. Over 150 vertebrae, and total length upwards of 1 m. Neural spines atrophied. The foremost ribs angularly bent, later ribs straight. Dermal armature not observed. Coal Measures; Kilkenny, Ireland, and (?) N. America. Lower Permian; Bohemia.

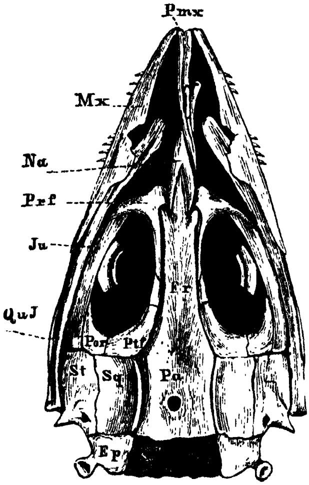


FIG. 323.
Dolichosoma longissimum Fritsch. Lower Permian; Nurschan, Bohemia. Restored. Lettering as in Fig. 313, etc. Three times nat. size (after Fritsch).

Ophiderpeton Huxley (*Thyrsidium* Cope) (Fig. 324). Skull imperfectly known, shorter and more obtuse than in *Dolichosoma*. Small polygonal plates on the cheek. Ribs resembling intermuscular bones of fishes, with dorsal and ventral processes. Ventral scutes small, oat-shaped; dorsal ossicles shagreen-like. *O. brownriggi* Huxley, from the Irish Coal Measures, 40-60 cm. long. Smaller species known from the Permian of Bohemia. *O. amphiuminus* Cope sp. Coal Measures; Linton, Ohio.

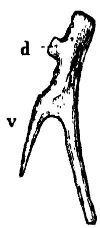


FIG. 324.
Ophiderpeton granulosum Fritsch. Rib. Permian; Bohemia. *d*, dorsal; *v*, ventral process. 1/6 (after Fritsch).

Family 6. Tuditanidae.[1]

Long-tailed Lepospondyli *approaching* Reptilia *in* T-*shaped interclavicle and slender abdominal ribs. Neural spines and chevrons of caudal vertebrae expanded distally and pectinated. Carpus and tarsus ossified in adult.* Upper Carboniferous and Lower Permian.

Sauravus Thevenin. Skull triangular, with rounded snout. Well-developed abdominal ribs. *S. costei* Thev. About 30 cm. in length. Upper Carboniferous; Blanzy (Saône-et-Loire), France. *S. cambrayi* Thev. Smaller. Lower Permian; Télots, near Autun, France.

Datheosaurus Schroeder. Head three-sided with rounded angles. Ischium and pubis on each side fused into a continuous plate; hind limbs comparatively stout. Abdominal ribs not yet observed. *D. macrurus* Schroed. Lower Permian; Neurode, Silesia.

Tuditanus Cope (*Eosauravus* Williston). Body long and slender with at least twenty-three presacral vertebrae. Phalangeal formula of hind foot, 2, 3, 4, 5, 4. *T. punctulatus* Cope. Coal Measures; Linton, Ohio, U.S.A.

Eusauropleura Romer. Coal Measures; Linton, Ohio.

[1] *Moodie, R. L.*, Carboniferous Air-breathing Vertebrates of the U.S. National Museum. Proc. U.S. Nat. Mus., vol. 37, p. 11 (*Isodectes punctulatus* Cope), 1909.—*Schroeder, H.*, *Datheosaurus macrurus* nov. gen. nov. sp. Jahrb. k. preuss. geol. Landesanst., vol. xxv., p. 282, 1905.—*Thevenin, A.*, Les plus anciens quadrupèdes de France. Ann. Paléont., vol. v., p. 42, 1910. Also *loc. cit.*, vol. i., p. 12, 1906.—*Williston, S. W.*, Bull. Geol. Soc. America, vol. xxi., p. 272, 1910.

Sub-Order 3. PHYLLOSPONDYLI. (*Branchiosauria.*)

Notochord persistent and not constricted, encased in imperfect barrel-shaped vertebrae formed by a pair of delicate hypocentra and downward prolongations of the neural arch, but without pleurocentra. Teeth simple, hollow.

Family 1. **Branchiosauridae.**[1]

Lizard-like Stegocephali *with broad, obtusely rounded head. Occipital region cartilaginous. Ribs short and straight, with simple, thickened proximal ends. Pubis not ossified. Manus with four, pes with five digits ; carpus and tarsus cartilaginous. Ventral scales thin, small, rounded, and arranged in regular series.* Carboniferous and Permian.

Branchiosaurus Fritsch (*Protriton, Pleuroneura* Gaudry) (Figs. 277, *A*, *B* ; 279, 280, 292, 294, 297, *A* ; 325, 326). Head about as broad as long, truncate behind, with shallow auditory notch, and very large elliptical orbits. Sclerotic ring of about 30 small plates, and also a supplementary series of smaller plates

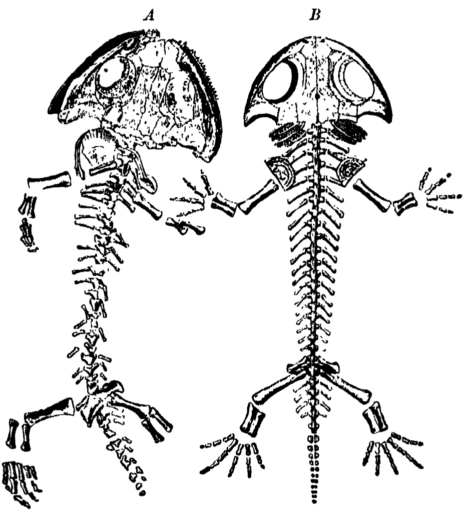


FIG. 325.

Branchiosaurus amblystomus Credner. Lower Permian (Rothliegendes); Niederhässlich, near Dresden. *A*, Skeleton of adult individual, one-half nat. size. *B*, Restoration of a larval form with gill arches, enlarged (after Credner).

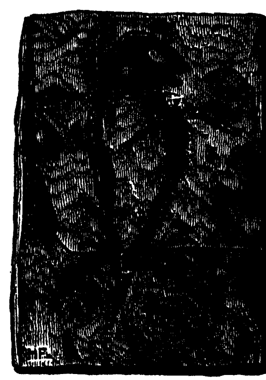


FIG. 326.

Branchiosaurus petrolei Gaudry sp. Lower Permian; Autun. Nat. size (after Gaudry).

irregularly arranged. Cranial plates radially striated or punctate. Parasphenoid greatly expanded behind, and uniting with trifid pterygoid. Vomer paired, the two pieces triangular; palatines imperfectly known. Jaws with a single series each of slender, closely spaced conical teeth. Interclavicle subrectangular, externally furrowed. Ilium stout, hourglass-shaped; ischium

[1] *Bulman, O. M. B.*, *Branchiosaurus* from Odernheim. Ann. Mag. Nat. Hist. [10], vol. i., p. 250, 1928.—*Bulman, O. M. B.*, and *Whittard, W. F.*, On *Branchiosaurus* and Allied Genera. Proc. Zool. Soc., 1926, p. 533.—*Jaekel, O.*, Körperform und Hautbedeckung von Stegocephalen. Sitzb. Ges. naturf. Freunde, Berlin, 1896, p. 1.—*Schönfeld, G.*, *Branchiosaurus tener* Schön. Isis, 1911, p. 19.—*Watson, D. M. S.*, *Eugyrinus wildi* (A.S.W.). Geol. Mag., 1921, p. 70.—*Whittard, W. F.*, Structure of *Branchiosaurus flagrifer* sp. n., etc. Ann. Mag. Nat. Hist. [10], vol. v., p. 500, 1930.

delicate, triangular. The entire ventral surface of the body, as well as a portion of the tail and limbs, was protected by deeply overlapping cycloidal scales (Fig. 277, *A*, *B*, p. 193) arranged in several distinct series. Functional gill arches are indicated in many immature examples by the regular series of minute denticles which were originally arranged on them. Tail known to have been about as long as trunk with the head, but most of the caudals unossified.

This genus and *Archegosaurus* are the commonest and best known examples of Palaeozoic Amphibians. Remains of *Branchiosaurus* are abundant in the fine-grained limestone of the Middle Rothliegendes near Dresden, where the small bones are clearly outlined in white against a greyish-coloured matrix. Credner's elaborate researches on the structure and development of this form were based on comparisons of over 1000 specimens. Several species occur also in the Lower Permian of Nürschan (Nyřan) and Kounova in Bohemia, Oberhof and Friedrichsroda in Thuringia, Odernheim in Rhenish Prussia, and Autun (Saône-et-Loire), France. At least one species also in the Coal Measures of Linton, Ohio, U.S.A. The adults of the largest species are about 12 cm. in length to the base of the soft tail.

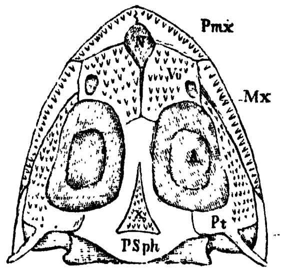


FIG. 327.

Palatal aspect of skull of *Acanthostoma vorax* Credner, restored. Lower Permian; Saxony. *A*, orbit; *N*, vacuity probably beneath intermaxillary gland; *Pmx*, premaxilla; *Mx*, maxilla; *Quj*, quadratojugal; *PSph*, parasphenoid; *Pt*, pterygoid; *Vo*, vomer, with internal narial opening wrongly surrounded by the bone. Nat. size (after Credner). For a different restoration see *Jaekel, O.*, Die Wirbeltiere, p. 113, fig. 127 (Berlin, 1911).

Pelosaurus Credner (Fig. 277, *D*). 18 to 20 cm. long. Skull relatively very large, with lachrymal in front of orbits, and no supplementary sclerotic plates. Lower Permian; Niederhässlich, near Dresden; Odernheim, Rhenish Prussia; and Autun, France. *P. laticeps* Credner.

Melanerpeton Fritsch (Fig. 297, *B*). 2·5 to 13 cm. long. Skull as in *Branchiosaurus*, but more produced posteriorly. Interclavicle extended into a long posterior process. A distinct dermal armouring not present, but quantities of small calcareous shagreen-like particles sometimes observed instead. Branchial arches present in young examples. Lower Permian of Braunau, Bohemia; Lhotka, Moravia; and Niederhässlich, Saxony.

Micrerpeton Moodie. Limbs comparatively stout; fore limb larger than hind limb. Tail deep and laterally compressed, with a median and dorsal sensory canal on each side, and apparently ornamented with vertical stripes. *M. caudatum* Moodie, about 5 cm. in length. Coal Measures; Mazon Creek, Illinois.

Eumicrerpeton Moodie. Eye elongate, close to edge of skull. Postero-lateral angle of skull sharp. Limb bones short and stout. Alimentary canal usually preserved in the fossils. *E. parvum* Moodie. Coal Measures; Mazon Creek.

Pelion Wyman. Coal Measures; Linton, Ohio.

Mazonerpeton Moodie. Coal Measures; Mazon Creek.

Eugyrinus Watson. Lower Coal Measures; Colne, Lancashire.

Leptorophus Bulman. Lower Permian; Saxony.

Micromelerpeton Bulman. Lower Permian; Odernheim, Rhenish Prussia.

Dawsonia Fritsch. Jaw-bones, vomer, palatines, and parasphenoid armed with teeth. Lower Permian; Bohemia.

Acanthostoma Credner (Fig. 327). Lower Permian; Niederhässlich, Saxony. All bones of palate bearing teeth.

The following imperfectly known genera from the Coal Measures of Linton, Ohio, seem to represent one or two allied families:—*Colosteus* Cope; *Erpetosaurus*, *Stegops* Moodie; *Branchiosauravus* Romer; *Platyrhinops*, *Mytaras* Steen. The skull of *Stegops* has postero-lateral cornua.

Sub-Order 4. ADELOSPONDYLI.[1] (*Lysorophia.*)

Vertebrae cylindrical, deeply amphicoelous, and pierced by a remnant of the notochord; neural arch separate; the bone traversed by irregular cavities. Ribs long and curved, usually with double head. Cranial roof over temporal region tending to be reduced; occipital condyle single; parasphenoid very large and broad; jaw relatively short. Branchial arches large and well ossified.

In those respects in which these small *Stegocephali* differ from the other members of the Order, they approach the *Urodela*, of which they may be the ancestors.

Family 1. Adelogyrinidae.

Head much elongated, with orbits far forwards; no tabular bones, but squamosals, quadrato-jugals, and jugals large; a pineal foramen. Lower Carboniferous.

Adelogyrinus Watson. External bones with pitted ornament. Orbits relatively large, extending as far backwards as the wide suture between the frontal and parietal bones. Squamosal produced backwards into a small horn. Very small blunt teeth in a regular close series. Ventral armour of slender rhomboidal scutes. *A. simorhynchus* Watson, with skull about 4·5 cm. long. Lower Carboniferous; Pentland Oil Works, Edinburgh.

Dolichoparcias Watson. Orbits much smaller, opposite anterior half of frontal bones, which meet the parietals only in the middle. The apex of the very small blunt teeth inclined backwards. *D. disjectus* Watson, with skull about 7 cm. long. Lower Carboniferous; Burdiehouse, Edinburgh.

Family 2. Lysorophidae.

Head much elongated, with orbits nearly median; temporal roof much reduced; tabular bones present; pineal foramen minute or absent. Upper Carboniferous and Lower Permian.

Lysorophus Cope (Fig. 328). Occiput and otic region well ossified; the exoccipital pierced by a foramen for the hypoglossal nerve, and having a small facet for articulation probably with a proatlas. Postorbital and jugal bones absent. No pineal foramen. Teeth acrodont, hollow cones, large on the

[1] *Broili, F.*, Systematische und biologische Bemerkungen zu der permischen Gattung *Lysorophus*. Anat. Anzeig., vol. xxxiii., p. 290, 1908.—*Case, E. C.*, Skull of *Lysorophus tricarinatus* Cope. Bull. Amer. Mus. Nat. Hist., vol. xxiv., p. 531, 1908.—*Finney, M.*, Limbs of *Lysorophus*. Journ. Morphology, vol. xxiii., p. 664, 1912.—*Sollas, W. J.*, Structure of *Lysorophus* as exposed by Serial Sections. Phil. Trans. Roy. Soc., vol. 209 B, p. 481, 1920.—*Watson, D. M. S.*, *Adelospondyli*. Palaeont. Hungarica, vol. i., p. 245, 1930.—*Williston, S. W.*, *Lysorophus*, a Permian Urodele. Biol. Bulletin, vol. xv., p. 229, 1908.

premaxilla, maxilla, and dentary. *L. tricarinatus* Cope, with skull usually about 2 cm. to 3 cm. long. Lower Permian; Illinois and Texas, U.S.A.

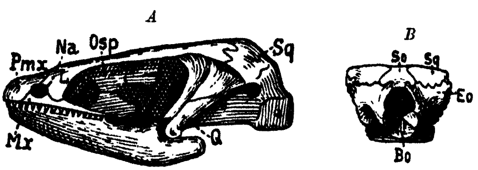


FIG. 828.

Lysorophus tricarinatus Cope. Skull in left side view (*A*) and occipital view (*B*). Permian; Texas. *Bo*, basioccipital; *Eo*, exoccipital; *L*, lachrymal; *Mx*, maxilla; *Na*, nasal; *Osp*, interorbital septum; *Pmx*, premaxilla; *Q*, quadrate and squamosal with supratemporal above; *So*, supraoccipital; *Sq*, tabular. About twice nat. size (*A* after Case, *B* after Broili. Nomenclature after Sollas).

Cocytinus Cope (*Brachydectes* Cope). ? *Pleuroptyx* Cope. Upper Carboniferous; Linton, Ohio, U.S.A.

Footprints of *Stegocephali*[1] are not uncommon in the Coal Measures of Nova Scotia, New Brunswick, Pennsylvania, Ohio, Kansas, Virginia, Saxony, and elsewhere. They occur also in the Permian of North America, Thuringia, Saxony, Bohemia, and England. One problematical specimen is known even from the Upper Devonian (Chemung) of Pennsylvania (*Thinopus antiquus* Marsh). The impressions always occur along stratification planes, and on removal of the superjacent layer the counterpart appears in relief, and is usually accompanied by a series of fossil mud-cracks. Most of these tracks are five-toed, although some occur in which the manus, which is of smaller size than the pes, has but four digits. Many footprints from the Trias often ascribed to *Stegocephali*, such as *Cheirotherium*, belong to Dinosaurs and other Reptiles.

Order 2. GYMNOPHIONA. (*Apoda* Oppel.)

Vermiform Amphibia *covered with small scales arranged in transverse rings. Vertebrae amphicoelous, with persistent notochord. Cranium ossified; maxillae and palatines with small, backwardly curved teeth. Ribs weakly developed. Pectoral and pelvic arches absent, and no limbs.*

The Coecilians constitute a small group restricted to the South American and Indo-African tropics, and are unknown in the fossil state.

[1] *Carman, J. E.*, Fossil Footprints from the Pennsylvanian System in Ohio. Bull. Geol. Soc. America, vol. 38, p. 385, 1927.—*Gilmore, C. W.*, Fossil Footprints from the Grand Canyon. Smithson. Misc. Coll., nos. 2832, 2917, 2956, 1926-28.—*Hardaker, W. H.*, Fossil-bearing Horizon in the "Permian" Rocks of Hamstead Quarries, near Birmingham. Quart. Journ. Geol. Soc., vol. lxviii., p. 639, 1912.—*Hausse, R.*, Fossile Tierfährten im unteren Rothliegenden des Steinkohlenbeckens im Plauenschen Grunde bei Dresden. Jahrb. Berg- u. Hüttenw. Sachsen, 1910, p. 3.—*Hickling, G.*, British Permian Footprints. Mem. Manchester Lit. and Phil. Soc., vol. lii., no. 22, 1909.—*Jaekel, O.*, Über die ältesten Gliedmassen von Tetrapoden. Sitzb. Ges. naturf. Freunde, Berlin, 1909, p. 587.—*Lull, R. S.*, Fossil Footprints from the Grand Canyon of the Colorado. Amer. Journ. Sci. [4], vol. xlv., p. 337, 1918.—*Martin, H. T.*, Gigantic Amphibian in the Coal Measures of Kansas. Kansas Univ. Sci. Bull., vol. xiii., p. 103, 1922.—*Matthew, G. F.*, Attempt to classify Palaeozoic Batrachian Footprints. Trans. Roy. Soc. Canada [2], vol. ix., sect. 4, p. 109, 1903.—Batrachian Footprints of the Carboniferous System in Eastern Canada. *Loc. cit.*, vol. x., p. 77, 1905.—*Moodie, R. L.*, Vertebrate Footprints from the Red Beds of Texas. Amer. Journ. Sci. [5], vol. xvii., p. 352, 1929; Journ. Geol., vol. xxxviii., p. 548, 1930.—*Morton, D. J.*, Footprint of *Thinopus antiquus*. Amer. Journ. Sci. [5], vol. xii., p. 409, 1926.—*Nopcsa, F.*, Die Familien der Reptilien, p. 129. Berlin, 1923.—*Pabst, W.*, Die Thierfährten in dem Rothliegenden Deutschlands. Nova Acta Acad. Caes. Leop.-Car., vol. lxxxix., p. 315, 1908.—*Schmidt, H.*, Stegocephalenfährte aus dem sächsischen Obercarbon. Palaeont. Zeitschr., vol. ix., p. 176, 1928.

Order 3. URODELA.[1] (*Caudata; Batrachia gradientia.*)

Elongate tailed Amphibia *with naked skin, usually with two pairs of short limbs, and with or without external gills. Roof of temporal region of skull reduced; no supraoccipital, postorbitals, and supratemporals. No pineal foramen. Vertebrae usually completely ossified. Ilio-sacral connection acetabular.*

Urodeles are distinguished from Stegocephalians chiefly by their naked body, solid vertebrae, usually short ribs, and peculiarities in the conformation of the skull and pectoral arch. The vertebrae may be either amphicoelous or opisthocoelous, are rarely pierced for the notochord, and have weakly developed spinous and transverse processes.

The *skull* in the existing forms (Fig. 329) is broad, flattened, and anteriorly rounded, and remains partly cartilaginous even in the adult, with both membrane and cartilage bones. The cranial roof is formed by the parietal, frontal, and prefrontal elements, adjoining which on either side are the large temporal fossae and orbits. The nasal capsule is sometimes covered by ossified nasals, and sometimes remains cartilaginous. The anterior and lateral margins of the skull are formed by the premaxillae and maxillae, but the latter are sometimes entirely wanting. In the basioccipital region only the exoccipitals are ossified, and the auditory capsule remains either cartilaginous or partially ossified, being covered by a thin, transversely elongated squamosal. Jugal and quadrato-jugal are absent, the quadrate is small, and only its articular extremity is ossified. Parasphenoid, vomers, and pterygoids are conspicuous on the under side of the skull, but the palatines are frequently atrophied. Small, acutely conical pleurodont teeth (Fig. 329) are present in both jaws, and also on the vomer and palatines.

The *pectoral arch* remains for the most part cartilaginous. Only the ventral portion of the scapula unites with the proximal ends of the coracoid and precoracoid to form a common osseous plate. In the *pelvic arch* only the ilium and large ischia are regularly ossified, the pubis remaining, as a rule, cartilaginous. The limbs do not differ essentially from those of Stegocephalians, and the carpus and tarsus exhibit various degrees of ossification.

Urodeles live in fresh water or in damp shady places on the land, subsisting on worms, gastropods, small aquatic animals, and fish spawn. Fossil remains occur usually in freshwater deposits, and are always very rare. Only

[1] *Adams, A.*, and *Martin, H. T.*, A New Urodele from the Lower Pliocene of Kansas. Amer. Journ. Sci. [5], vol. xvii., p. 504, 1929.—*Bolkay, St. J.*, Schädel der Salamandrinen. Zeitschr. f. Anat. u. Entwicklungs., vol. 86, p. 259, 1928.—*D'Erasmo, G.*, Fauna dei calcari di Pietraroia. Palaeont. Italica, vol. xxi., p. 56, 1915.—*Dollo, L.*, Note sur le Batracien de Bernissart. Bull. Mus. Roy. Hist. Nat. Belg., vol. iii., p. 85, 1884 [*Hylaeobatrachus*].—*Laube, G. C.*, Andriasreste aus der böhmischen Braunkohlenformation. Abhandl. deutsch. naturw. Ver. "Lotos," vol. i., pt. 2, p. 1, 1897.—Amphibienreste aus dem Diatomaceenschiefer von Sulloditz. *Loc. cit.*, vol. i., pt. 3, p. 1, 1898. —Also *loc. cit.*, vol. ii., pt. 4, p. 52, 1901.—*Liebus, A.*, Neue *Andrias*-Reste aus dem böhmischen Tertiär. Palaeont. Zeitschr., vol. xi., p. 102, 1929.—*Meyer, H. von*, Zur Fauna der Vorwelt, pt. 2. Frankfurt, 1845.—Salamandrinen aus der Braunkohle, etc. Palaeontogr., vol. vii., p. 46, 1860; also vol. ii, p. 70, and vol. x., p. 292.—*Moodie, R. L.*, The Ancestry of the Caudate Amphibia. Amer. Nat., vol. xlii., p. 361, 1908.—*Noble, G. K.*, Two new fossil Amphibia from the Miocene of Europe. Amer. Mus. Novitates, no. 303, 1928.—*Stefano, G. de*, Sui batraci urodeli delle Fosforiti del Quercy. Boll. Soc. Geol. Ital., vol. xxii., p. 40, 1903.—*Strauch, A.*, Revision der Salamandridengattungen. St. Petersburg, 1870.—*Wiedersheim, R.*, *Salamandrina perspicillata*, Versuch einer vergleichenden Anatomie der Salamandrinen. Würzburg, 1875.—Das Kopfskelet der Urodelen. Leipzig, 1877.

three Mesozoic skeletons are known, and the few Tertiary genera are scarcely distinguishable from those now living.

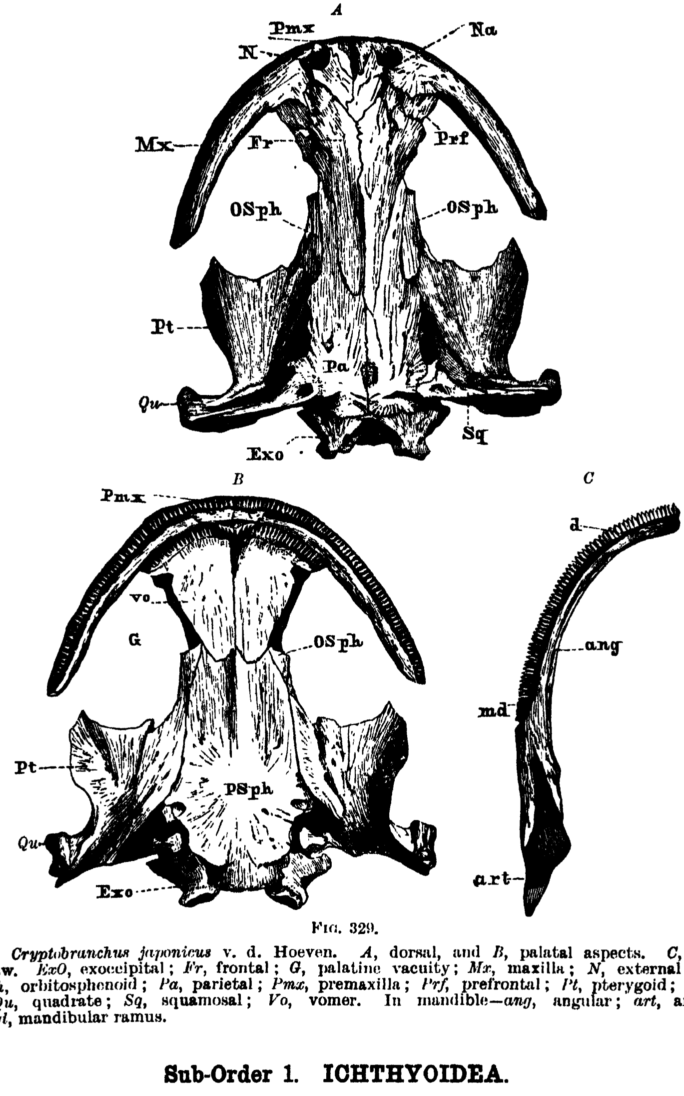


FIG. 329.

Skull of *Cryptobranchus japonicus* v. d. Hoeven. *A*, dorsal, and *B*, palatal aspects. *C*, left ramus of lower jaw. *ExO*, exoccipital; *Fr*, frontal; *G*, palatine vacuity; *Mx*, maxilla; *N*, external nares; *Na*, nasal; *OSph*, orbitosphenoid; *Pa*, parietal; *Pmx*, premaxilla; *Prf*, prefrontal; *Pt*, pterygoid; *PSph*, parasphenoid; *Qu*, quadrate; *Sq*, squamosal; *Vo*, vomer. In mandible—*ang*, angular; *art*, articular; *d*, dentary; *md*, mandibular ramus.

Sub-Order 1. ICHTHYOIDEA.

Vertebrae amphicoelous, with persistent remnants of notochord. Three pairs of persistent external gills, or in their absence a branchial aperture. Eyes small, without distinct lids. Living in water.

To this group probably belong the unique skeleton of *Hylaeobatrachus croyi* Dollo, from the Wealden of Bernissart, Belgium, the earliest known typical Urodele; and also the giant salamander from the Upper Miocene of Oeningen, Baden (*Andrias scheuchzeri* Tschudi, Fig. 330), originally described by Scheuchzer

as *Homo diluvii testis*. The latter species attains a length of about 1 m., and differs but slightly from the recent *Cryptobranchus* v.d. Hoeven (*Megalobatrachus* Tschudi) of Japan. A somewhat smaller species (*Andrias tschudii* v. Meyer) occurs in the Miocene lignite of Rott, near Bonn; and *Andrias bohemicus* Laube is found in the Upper Oligocene lignite of Bohemia. *Orthophyia* H. von Meyer, from the Upper Miocene of Oeningen, Baden, is of doubtful affinities. *Plicagnathus* H. J. Cook is the name of jaws from the Lower Pliocene of Nebraska, U.S.A. The systematic position of *Hemitrypus* Cope and *Scapherpeton* Cope, from the Upper Cretaceous of Montana, U.S.A., and Alberta, Canada, is uncertain (L. M. Lambe, Contrib. Canad. Palaeont., vol. iii., p. 31, 1902).

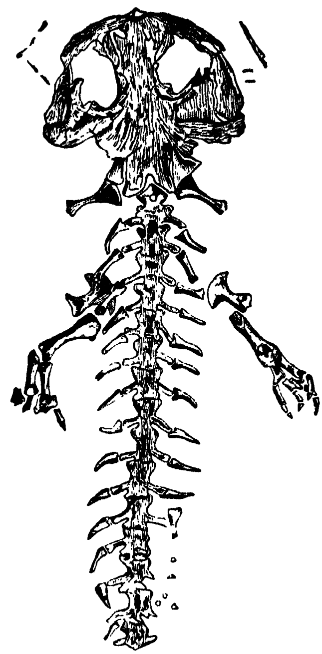


FIG. 330.
Andrias scheuchzeri Tschudi. Upper Miocene; Oeningen, Baden. 1/6 nat. size.

Sub-Order 2. SALAMANDRINA.

Vertebrae amphicoelous, rarely opisthocoelous, completely ossified. Without gills or gill aperture; well-developed eyelids always present. Maxillae present; both jaws toothed.

Several genera resembling recent newts and salamanders occur sparsely in the Cretaceous of Pietraroja, Prov. Benevento, Italy; Oligocene of Quercy and Miocene of Sansan in France; Upper Miocene of Oeningen, Baden, and of Teruel in Spain; Lower Miocene of Rott and Erpel, near Bonn; and the Bohemian Tertiary. Among these may be mentioned *Polysemia*, *Heliarchon*, and *Archaeotriton* v. Meyer; *Megalotriton* Zittel; *Heteroclitotriton* de Stefano; *Oligosemia* Navás; *Chelotriton* Pomel; *Tylototriton* Anderson; and possibly *Molge* (*Triton*) itself. *Plioamblystoma* Adams, from the Lower Pliocene of Sherman Co., Kansas, is related to the existing *Amblystoma* Tschudi.

Footprints which may be Salamandrine occur in the Fort Union Beds (Paleocene) of Montana (*Ammobatrachus montanensis* C. W. Gilmore, Proc. U.S. Nat. Mus., vol. 74, art. 5, 1928).

Order 4. ANURA.[1] (*Ecaudata; Batrachia salientia.*)

Naked, tailless, short and broad Amphibia, *with vertebrae usually procoelous. Caudal vertebrae coalesced into a slender elongate piece, or coccyx. Pubis and ischium*

[1] *Bolkay, St. J.*, Additions to the Fossil Herpetology of Hungary from the Pannonian and Praeglacial Period. Jahrb. k. ungar. geol. Reichsanst., vol. xxi., p. 117, 1913.—*Boulenger, G. A.*, The Occurrence of *Discoglossus* in the Lower Miocene of Germany. Ann. Mag. Nat. Hist. [6], vol. viii., p. 83, 1891.—*Camp, C. L.*, Extinct Toad from Rancho La Brea. Bull. Dept. Geol. Univ. California, vol. x., p. 287, 1917.—*Fejérváry, G. J. de*, *Rana méhelyi*. Jahrb. k. ungar. geol. Reichsanst., vol. xxiii., p. 133, 1916.—Anoures fossiles des couches préglaciaires de Püspökfürdö en Hongrie. Földtani Közlony, vol. xlvii., p. 1, 1917.—Osteologie, Phylogenie, und Systematik der Anuren. Archiv f. Naturgesch., vol. lxxxvii., pt. 3, p. 1, 1921.—*Fraas, E.*, *Rana danubiana* H. v. Meyer var. *rara* O. Fraas aus dem Obermiocän von Steinheim. Jahresh. Vereins f. vaterl.

fused. Ilio-sacral attachment extremely pre-acetabular. Carpus and tarsus ossified, and the two bones forming the proximal row of the latter greatly elongated. Development by metamorphosis. No gills in the adult.

The vertebral column consists in the adult of from ten to twelve usually procoelous vertebrae, all of which with the exception of atlas and coccyx bear stout transverse processes. Short ribs are present only in the *Discoglossidae*. All the post-sacral vertebrae become fused during metamorphosis into a single caudal piece, the coccyx or urostyle (Fig. 331).

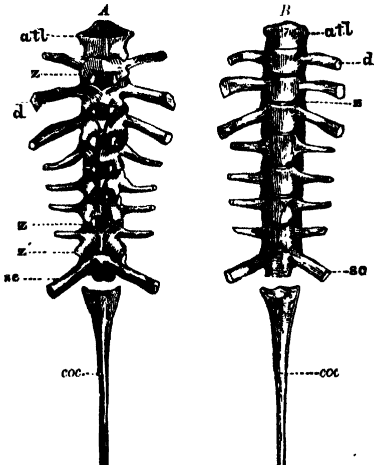


Fig. 331.

Vertebral column of *Rana esculenta* Linn. *A*, dorsal; and *B*, ventral aspect. *atl*, atlas; *coc*, coccyx; *d*, transverse process; *sc*, sacral vertebra; *z*, anterior, and *z'*, posterior zygapophyses. Nat. size.

The *skull* (Fig. 332) is flattened, with very large orbits. Parietals and frontals are fused into an elongated pair of median elements, in front of which lie the ring-shaped sphenethmoid (or orbitosphenoid) and nasals. The basioccipital region and auditory capsules are ossified; the parasphenoid is T-shaped; and the pterygoid, palatine, and jugal are well developed, the last-named joining the maxilla in front and quadrato-jugal behind. Small, bristle-like pleurodont teeth occur on the jaw-bones and vomer, or may be entirely wanting.

The *pectoral arch* (Fig. 333) is remarkable for its large scapular element, which is commonly divided and incompletely ossified, and joins the coracoid and clavicle. The sternum is also large and more or less cartilaginous; of its three ossified portions, the anterior is called the omosternum; the middle piece is the sternum proper; and the posterior, which terminates in a semicircular cartilaginous expansion, is the xiphisternum. Ulna and radius are fused, the two rows of small carpals are ossified, and the manus has four digits.

Naturk. Württ., 1903, no. 25.—*Haughton, S. H.*, Fossil Frogs from the Clays at Banke. Trans. Roy. Soc. S. Africa, vol. xix., p. 233, 1931.—*Meyer, H. von*, Zur Fauna der Vorwelt, pt. 1. Frankfurt, 1845.—Also articles in Palaeontogr., vol. ii., p. 70; vol. vii., p. 46; and Neues Jahrb. für Min., etc., 1843, pp. 395, 580; 1845, p. 798; 1846, p. 351; 1847, p. 192; 1851, p. 78; 1852, pp. 57, 465; 1853, p. 162; 1858, p. 202; and 1863, p. 187.—*Moodie, R. L.*, An American Jurassic Frog. Amer. Journ. Sci., vol. xxxiv., p. 286, 1912.—Fossil Frogs of North America. *Loc. cit.*, vol. xxxviii., p. 531, 1914.—*Navás, R. P. L.*, Algunos fósiles de Libros (Teruel). Bol. Soc. Iberica de Cien. Nat., vol. xxi., p. 52, 1922.—*Noble, G. K.*, New Spadefoot Toad from the Oligocene of Mongolia, with a Summary of the Evolution of the *Pelobatidae*. Amer. Mus. Novit., no. 132, 1924. See also *loc. cit.*, nos. 303, 1928; 401, 1930.—*Parker, H. W.*, Two Fossil Frogs from the Lower Miocene of Europe. Ann. Mag. Nat. Hist. [10], vol. iv., p. 270, 1929. See also *loc. cit.*, vol. vi., p. 201, 1930.—*Piveteau, J.*, Quelques amphibiens anoures. Ann. Paléont., vol. xvi., p. 61, 1927.—*Portis, A.*, Resti di batrachii fossili Italiani. Atti R. Accad. Torino, vol. xx., p. 1173, 1885.—*Riabinin, A. N.*, Ein fossiler Frosch aus Transkaukasien. Proc. Russ. Palaeont. Soc., vol. vii., p. 87, 1928 [in Russian].—*Vidal, L. M.*, Sobre la presencia del tramo Kimeridgense en el Montsech y hallazgo de un batracio en sus hiladas. Mem. R. Acad. Ciencias, Barcelona [3], vol. iv., no. 18, 1902.—*Westenhöfer, M.*, Morphogenese der Anuren. Sitzungsb. Ges. naturf. Freunde, Berlin, 1929, p. 81.—*Wolterstorff, W.*, Über fossile Frösche insbesondere *Palaeobatrachus* [with complete bibliography]. Jahresb. Naturw. Vereins Magdeburg für 1885, '86, 1886–87.—Über fossile Frösche aus der Papierkohle von Burgbrohl (Laacher See). Jahrb. preuss. geol. Landesanst. Berlin, vol. xlix., p. 918, 1929.

The three elements of the *pelvic arch* are coössified at the acetabulum on either side to form a single piece, which joins its fellow in a median symphysis. Tibia and fibula are fused, the two bones forming the proximal row of the

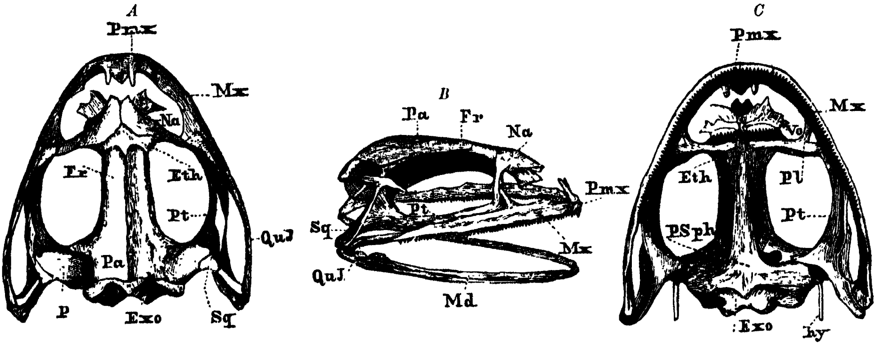


FIG. 332.

Skull of *Rana esculenta* Linn. *A*, From above. *B*, From the side. *C*, From below. *Eth*, sphenethmoid (orbitosphenoid); *Exo*, exoccipital; *FrPa*, fronto-parietal; *hy*, hyoid; *Md*, lower jaw; *Mx*, maxilla; *Na*, nasal; *P*, petrosal; *Pl*, palatine; *Pmx*, premaxilla; *PSph*, parasphenoid; *Pt*, pterygoid; *QuJ*, quadrato-jugal; *Sq*, squamosal (tympanic); *Vo*, vomer. Nat. size.

tarsus (astragalus and calcaneum) are much elongated, and the pes has five digits.

Fossil *Anura* are rare, the oldest known remains occurring in the Upper Jurassic of the Montsech, Lérida, Spain (*Montsechobatrachus* Fejérváry), and of Wyoming, U.S.A. (*Eobatrachus* Marsh). Another genus (*Stremmeia* Nopcsa) may perhaps be represented by fused carpal bones from the Upper Jurassic or Lower Cretaceous of Tendaguru, Tanganyika Territory, East Africa. Others are found in the Upper Eocene of India (*Oxyglossus pusillus* Owen sp.) and Wyoming. A few genera are known from the Upper Eocene, Oligocene, and Miocene of Southern France, Spain, Northern Italy, Germany, and Transcaucasia, *Rana*, *Discoglossus*, and the extinct *Palaeobatrachus* Tschudi and *Protopelobates* Bieber being the commonest forms. *Asphaerion* H. von Meyer, from the Miocene of Bohemia, seems to be related to *Rana*. Phosphatised mummies both of *Rana* and *Bufo* occur in the Oligocene Phosphorites of Quercy, France. The extinct *Macropelobates* Noble is found in the Oligocene of Mongolia. The Miocene lignites near Bonn yield not only numerous perfect skeletons, but impressions of tadpoles belonging to the genus *Palaeobatrachus* Tschudi (Figs. 334, 335); also skeletons of the allied genus *Lithobatrachus* Parker (referred to *Hyla* by Noble), and an extinct genus of *Pelobatidae*, *Eopelobates* Parker. Skeletons of an extinct genus *Eoxenopoides* Haughton occur in the Lower Tertiary, and skulls of *Xenopus stromeri* Ahl in the Middle Tertiary of Namaqualand, S.-W. Africa.

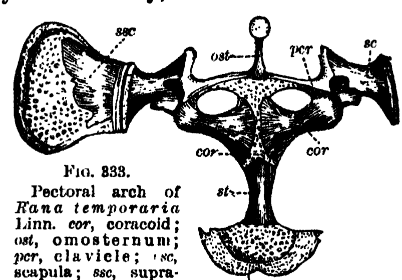


FIG. 333.
Pectoral arch of *Rana temporaria* Linn. *cor*, coracoid; *ost*, omosternum; *pcr*, clavicle; *sc*, scapula; *ssc*, suprascapula; *st*, sternum; *Xst*, xiphisternum. (Dotted parts cartilaginous.)

Complete skeletons of large toads (*Latonia seyfriedi* v. Meyer; *Pelophilus agassizi* Tschudi) are known from the Upper Miocene freshwater marls of

Oeningen, Baden. The equivalent deposits of Günzburg, Steinheim, Sansan, and Sinigaglia likewise yield remains of *Anura* (*Ranavus*, *Bufavus* Portis, etc.).

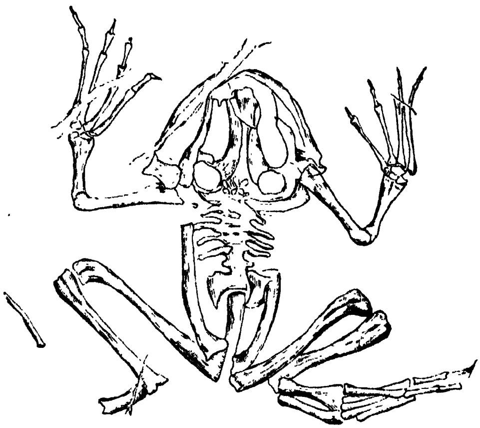


FIG. 334.
Palaeobatrachus grandipes Giebel. Lignite; Orsberg in Siebengebirge. $^2/_3$ nat. size (after Wolterstorff).

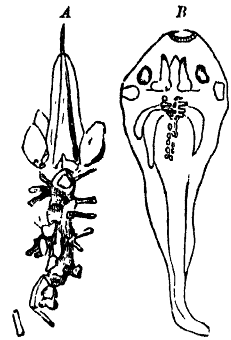
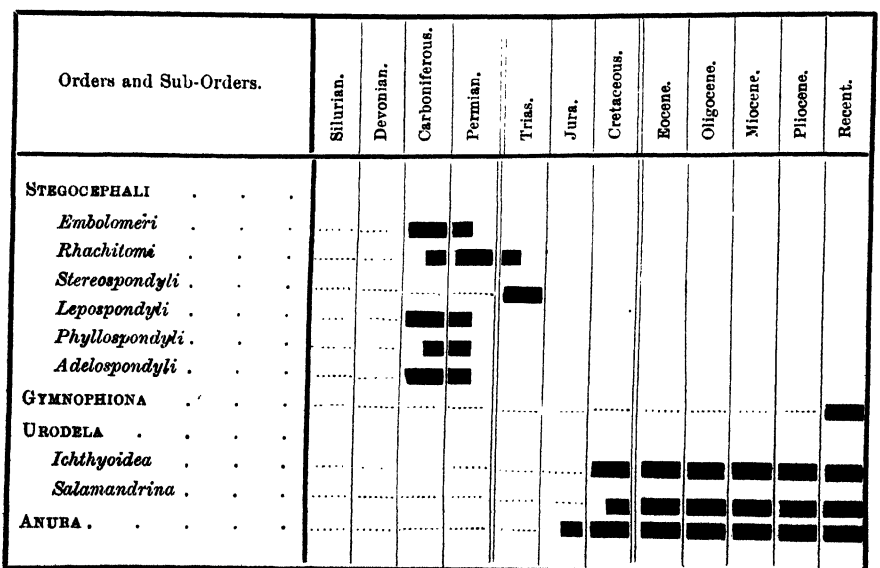


FIG. 335.
Larvae of *Palaeobatrachus fritschii* Wolterstorff. Miocene Lignites; Kaltennordheim, Rhön. Nat. size (after Wolterstorff and Mayer).

Pliocene and Pleistocene *Anura* belong chiefly to recent genera, but *Diplopelturus* Depéret is an extinct genus in the Pliocene of Rousillon, France, *Platosphus* de l'Isle in the Lower Pleistocene of Durfort (Gard), France, and *Pliobatrachus* Fejérváry in Pre-glacial deposits in Hungary.

Bufo occurs in the asphalt deposit of Rancho La Brea, California.

VERTICAL RANGE OF AMPHIBIANS.



Class 3. REPTILIA.[1]

Cold-blooded, naked, scaly or armoured vertebrates, breathing exclusively by lungs, and living on land or in water. Embryo with amnion and allantois, development without metamorphosis. Heart with two auricles, but usually with the ventricle incompletely divided. Skeleton completely ossified. Skull usually with a single basi-occipital condyle; mandible of several bones. Two pairs of limbs usually present; metapodial bones separate.

In external appearance (Fig. 336) most of the existing Reptiles closely resemble Amphibians, but are much more differentiated as a class, and are mostly of greater size. Among extinct Reptiles the limbs exhibit great diversity in structure and function. Among the *Pterosauria* the anterior limb is transformed into a flying organ with a flexible wing membrane; among Dinosaurs the appendicular skeleton attains a size and stoutness unsurpassed by the largest land mammals; in marine Reptiles the limbs are paddle-shaped; and in most Lacertilians, Theromorphs, Crocodiles, and Dinosaurs the limbs are for walking and running; while the only limbless forms occur among the *Squamata* (snakes and certain lizards).

The *integument* of Reptiles is tougher than that of Amphibians, and an exoskeleton is often developed by the ossification of the cutis and cornification of the epidermis. The former may give rise to bony scutes overlapping one another in a tectiform manner, or to larger bony plates with closely applied edges, arranged so as to form a more or less continuous shield, as in tortoises.

The *vertebral column* is always ossified, although remnants of the notochord may persist in the centra. In all cases where both pairs of limbs are present, cervical, dorsal, sacral, and caudal regions are distinguishable, and the dorsal series may be often subdivided into thoracic and lumbar vertebrae. The vertebral centra exhibit all gradations between *amphiplatyan* (flat-ended),

[1] *Adams, L. A.*, Phylogeny of the Jaw Muscles in Recent and Fossil Vertebrates. Ann. New York Acad. Sci., vol. xxviii., p. 51, 1919.—*Baur, G.*, Phylogenetic arrangement of the Sauropsida. Journ. Morphol., vol. i., p. 93, 1887.—Bemerkungen über die Osteologie der Schläfengegend der höheren Wirbeltiere. Anat. Anz., vol. x., p. 315, 1894.—*Broom, R.*, Temporal arches of the Reptilia. Proc. Zool. Soc., 1922, p. 17.—*Cope, E. D.*, On the homologies of the posterior cranial arches in the Reptilia. Trans. Amer. Phil. Soc., vol. xvii., p. 11, 1892.—*Fürbringer, M.*, Zur vergleichenden Anatomie des Brustschulterapparats und der Schultermuskeln. IV. Teil. Zeitschr. für Naturwissensch., vol. xxxiv., 1900.—*Gadow, H.*, Amphibia and Reptilia. Cambridge Nat. Hist., vol. viii., 1901.—*Goodrich, E. S.*, Classification of the Reptilia. Proc. Roy. Soc., vol. lxxxix. B, p. 261, 1916.—*Gregory, W. K.*, and *Camp, C. L.*, Studies in Comparative Myology and Osteology. Bull. Amer. Mus. Nat. Hist., vol. xxxviii., p. 447, 1918; see also vol. xlii., p. 95, 1920.—*Lydekker, R.*, Catalogue of the fossil Reptilia and Amphibia in the British Museum, vols. i.-iv. London, 1888-90.—*Meyer, H. von*, Zur Fauna der Vorwelt, pts. i.-iv. Frankfurt, 1845-60.—*Nopcsa, F.*, Die Familien der Reptilien. Fortschritte der Geol. u. Palaeont. Berlin, 1923.—The Genera of Reptiles. Palaeobiologica, vol. i., p. 163, 1928.—*Osborn, H. F.*, The Reptilian Subclasses Diapsida and Synapsida and the Early History of the Diaptosauria. Mem. Amer. Mus. Nat. Hist., vol. i., p. 451, 1903.—*Owen, R.*, Report on British Fossil Reptilia. Rep. Brit. Assoc. Adv. Sci., 9th Meet., p. 43, 1839. Also *ibid.*, 11th Meet., p. 60, 1841.—A History of British Fossil Reptiles. London, 1849-84.—*Van Straelen, V.*, Les œufs de reptiles fossiles. Palaeobiologica, vol. i., p. 295, 1928.—*Versluys, J.*, Das Streptostylie-Problem. Zool. Jahrb., Suppl. xv., p. 545, 1912.—Phylogenie der Schläfengruben und Jochbogen bei den Reptilia. Sitzb. Heidelberg. Akad. Wiss., math.-naturw. Kl. B, 1919, Abh. 13.—*Watson, D. M. S.*, Sketch classification of the Pre-Jurassic Tetrapod Vertebrates. Proc. Zool. Soc., 1917, p. 167.—*Williston, S. W.*, American Permian Vertebrates. Chicago, 1911.—Water Reptiles of the Past and Present. Chicago, 1914.—Phylogeny and Classification of Reptiles. Journ. Geol., vol. xxv., p. 411, 1917.—Osteology of the Reptiles, ed. W. K. Gregory. Cambridge, Mass., 1925.

amphicoelous (hollow-ended), *procoelous* (hollow in front, ball behind), and *opisthocoelous* (hollow behind, ball in front); and the union between the centra and their neural arches may be cartilaginous, sutural, or by anchylosis. The neural spines are always ossified. Sometimes they are enormously produced, in other cases (*Chelonia*) laterally expanded and united with dermal plates. The anterior zygapophyses have facets looking inward and upward, which are overridden by the post-zygapophyses of the vertebra immediately in front; and in the *Squamata* and *Dinosauria* the vertebrae are still further joined by a median process given off from the anterior (*zygosphene*) or posterior (*hyposphene*) end of the neural arch, and received into a notch of the arch next in front (*zygantrum*) or behind (*hypantrum*). The cervicals generally bear short transverse processes (*diapophyses*) attached to the sides of the centra, but in the dorsal series these processes are usually given off from the neural arches. In the cervicals also there is sometimes a single or paired process from the lower face of the centrum (*hypapophysis*). The haemapophyses of the caudal series form *chevron bones*, of which the two halves often unite in a single piece. The two foremost cervical vertebrae, the *atlas* and *axis* (or *epistropheus*), are closely connected and differ much from all the other vertebrae, being specially adapted to give free movement to the head (Fig. 337). The body or centrum of the atlas is firmly connected or fused with that of the axis, forming the *odontoid process* of the axis. The atlas thus usually becomes ring-shaped, being formed by the neural arch meeting or fused with a ventral wedge-bone or intercentrum. The bony ring is crossed by a strand of connective tissue, which separates the upper passage for the spinal chord from the lower space into which the odontoid process projects. Between the neural arch of the atlas and the occiput there is often a more or less vestigial neural arch, the *proatlas*. Among existing Reptiles there are never more than two sacral vertebrae, but the sacrum of Dinosaurs sometimes comprises as many as ten, and that of Pterosaurs from four to seven vertebrae. When more than three are present, however, they are usually coössified into a single piece (*synsacrum*). Only among Ophidians, Pythonomorphs, and Ichthyosaurs is there no differentiated sacral region. Small wedge-shaped

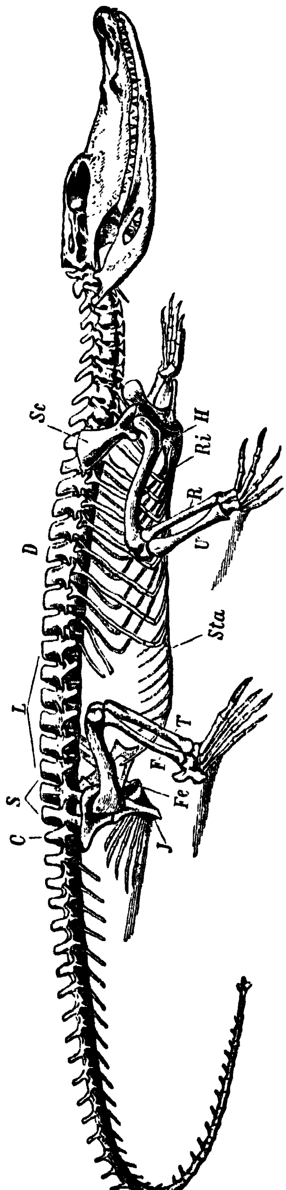


FIG. 336. Skeleton of Crocodile. *C*, first caudal vertebra; *D*, dorsal region; *F*, fibula; *Fe*, femur; *H*, humerus; *J*, ischium; *L*, lumbar region; *R*, radius; *Ri*, ribs; *S*, two sacral vertebrae; *Sc*, scapula; *Sta*, abdominal ribs (gastralia); *T*, tibia; *U*, ulna (after Claus).

intercentra (*hypocentra*) may be inserted between the cervicals, caudals, and a portion or all of the dorsals.

All the vertebrae with the exception of the posterior caudals may bear ribs. Cervical ribs are as a rule short, and in some groups have the distal end expanded in hatchet-shaped fashion. When a sternum is present, the ribs with which it is connected facilitate the distinction between cervical and dorsal regions. The posterior dorsal ribs have free extremities, and lumbar vertebrae are usually without ribs. Cervical ribs are usually double-headed, and the centra exhibit two facets for their attachment. Dorsal ribs may be either single- or double-headed, and in Chelonians are remarkable for their union with the broad costal plates of the carapace. In a double-headed rib (Fig. 338) the lower articulation is described as the *capitulum*, the upper as the *tuberculum*. Many of the *Reptilia* develop so-called abdominal ribs, or *gastralia*, which are ossifications of the connective tissue, and correspond to the ventral scutes of Stegocephalians.

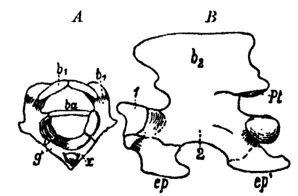


FIG. 337.

Atlas and axis of *Varanus*, the atlas in front view (*A*), the axis in left side view (*B*). b_1, b_2, neural arch of atlas and axis respectively; *ba*, band beneath the spinal chord and above the space for the odontoid process; *ep*, ep_1, two unpaired epiphyses or wedge-bones beneath the axis; *g*, articular surface for occipital condyle; *Pt*, postzygapophysis; *x*, unpaired wedge-bone completing the atlas below; *1*, centrum of the atlas (odontoid process of axis); *2*, centrum of axis (after Boas).

The *skull* (Fig. 339) agrees more nearly with that of Birds than that of Amphibians in its general features, and the ossification of the primordial cranium is much more extensive than in the latter group. The investing membrane bones are so intimately united with true cartilage bones that a distinction is often impossible. The basiocciput usually articulates with the atlas by means of a single, sometimes tripartite condyle, formed either by the basioccipital alone, or by this bone in conjunction with the exoccipitals. In some *Theromorpha* the exoccipitals alone form a pair of condyles. Both the basioccipital and supraoccipital may be excluded from the border of the *foramen magnum*. Of the bones forming the auditory capsule, the proötic (petrosal) is situated in front of the lateral parts of the occipital region; it occurs as a separate bone, and its front margin is pierced for the third branch of the trigeminal nerve. The opisthotic (paroccipital) is often fused with the exoccipital, and the epiotic with the supraoccipital. Besides the usual auditory opening, or *fenestra ovalis*, there is commonly a *fenestra rotunda;* the position of the former is usually between the opisthotic and proötic. A bony columella auris (stapes) is present. At the base of the skull immediately in front of the basioccipital occurs the basisphenoid, a true cartilage bone, continued forwards by a rudiment of the parasphenoid.

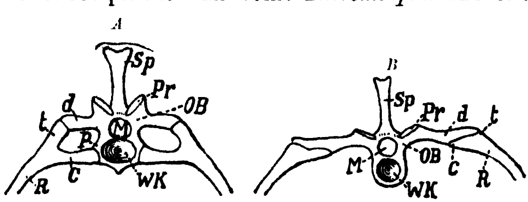


FIG. 338.

Anterior (*A*) and posterior (*B*) dorsal vertebra of *Alligator lucius*, front view. *C*, capitulum of rib; *d*, transverse process (diapophysis); *M*, canal for spinal chord; *OB*, neural arch; *P*, parapophysis; *Pr*, prezygapophysis; *R*, rib; *Sp*, neural spine; *t*, tuberculum of rib; *WK*, centrum (after Gegenbaur).

Alisphenoids and orbitosphenoids are as a rule wanting, or are replaced by downwardly directed processes of the parietals and frontals. The last-named bones are usually of large size, and may be either paired or unpaired.

Applied to the parietals on either side is a large squamosal, which takes part in the posterior cranial border and that of the supratemporal vacuity. The lower end of the squamosal usually abuts against the quadrate, which bears a condyle for articulation with the lower jaw. Sometimes the squamosal is divided, the upper portion being named supratemporal or prosquamosal. Behind the parietals and squamosals along the occipital border there are often various remnants of the postparietal (or interparietal) and tabular bones, which are so conspicuous in the Stegocephalians. They sometimes extend the cranial roof, sometimes turn downwards on the occipital face.

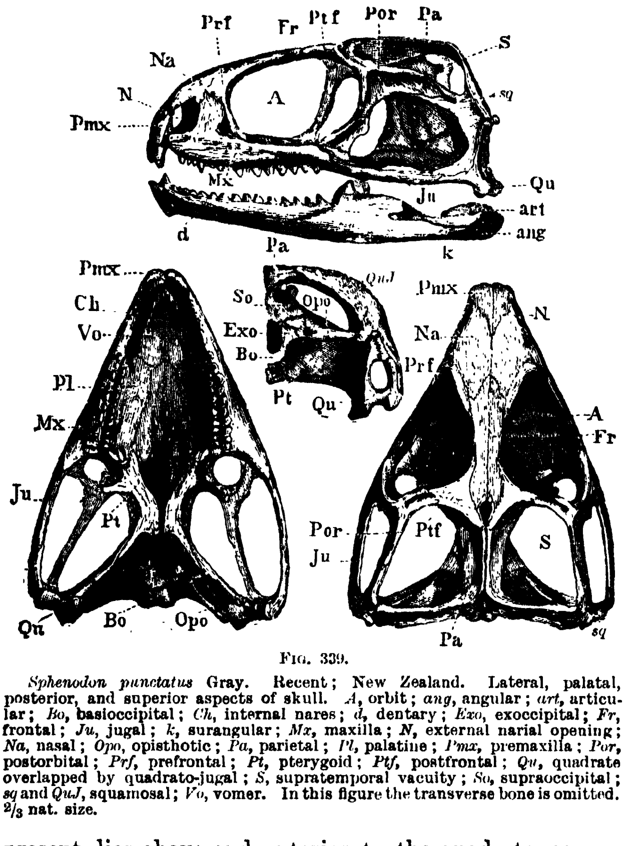


Fig. 339.

Sphenodon punctatus Gray. Recent; New Zealand. Lateral, palatal, posterior, and superior aspects of skull. *A*, orbit; *ang*, angular; *art*, articular; *Bo*, basioccipital; *Ch*, internal nares; *d*, dentary; *Exo*, exoccipital; *Fr*, frontal; *Ju*, jugal; *k*, surangular; *Mx*, maxilla; *N*, external narial opening; *Na*, nasal; *Opo*, opisthotic; *Pa*, parietal; *Pl*, palatine; *Pmx*, premaxilla; *Por*, postorbital; *Prf*, prefrontal; *Pt*, pterygoid; *Ptf*, postfrontal; *Qu*, quadrate overlapped by quadrato-jugal; *S*, supratemporal vacuity; *So*, supraoccipital; *sq* and *QuJ*, squamosal; *Vo*, vomer. In this figure the transverse bone is omitted. 2/3 nat. size.

Among the *Squamata* the quadrate is movably articulated with the squamosal, being united by ligaments only (*Streptostylica*); but among other Reptiles it is usually attached to the skull by suture (*Monimostylica*). The quadrato-jugal, when present, lies above and anterior to the quadrate, connecting it with the jugal. The latter joins the hinder end of the maxilla, and forms with it the inferior border of the orbit. The bony arcade separating the orbits and temporal fossae is formed either by the postorbital alone, or by that bone in connection with the postfrontal and jugal. The prefrontals are usually well developed, and adjoin the frontals on either side; sometimes they exclude the latter from the superior border of the orbit, and they join the lachrymals in forming its anterior border. In the most primitive Reptiles the lachrymals extend as far forwards as the external nares. The nasal capsules are roofed by the prefrontals and nasals, and bounded anteriorly by the paired or unpaired premaxillae. The latter, with the maxillae, complete the front rim of the upper jaw. A small membrane bone, the septomaxillary, often occurs within the narial cavity (*Squamata, Theromorpha, Cotylosauria*) on each side as a roof to Jacobson's organ, and in many *Theromorpha* it extends on the face.

In the palate the pterygoids form the connection between the quadrates,

basisphenoid, palatines, and vomers. They vary considerably in size and shape among the different Orders, according as the quadrate and maxillo-palatine apparatus are movably or rigidly united with the wall of the skull. In many forms a transverse bone (ectopterygoid) is developed between the pterygoid and maxilla, and a slender column-like bone, the columella or epipterygoid, extends between the parietal and pterygoid (Fig. 427). Sometimes a flat expansion of the maxillae joins the palatines, and enters with these bones, the vomers, premaxillae, and pterygoids into the formation of a secondary bony palate. According to Broom, the parasphenoid corresponds with the vomer in Mammals, and the bones commonly named vomers in Reptiles should be known as prevomers. The lower jaw is composed, as in Amphibians, of a dentary, splenial, coronoid, angular, and surangular formed from membrane ossifications, and an articular formed from Meckel's cartilage. There are also sometimes prearticular and postsplenial membrane bones. Crocodiles have the lower jaw as well as many of the cranial bones hollow and pneumatic.

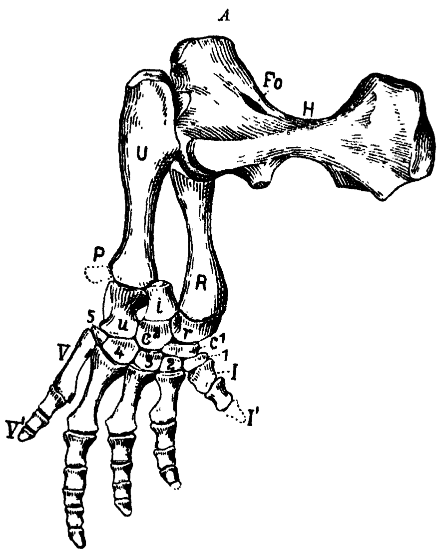
Teeth are wanting only among all but the earliest Chelonians and isolated representatives of other groups. As a rule they occur extensively on the margin of the jaw, and in some cases also on the palatines, pterygoids, and vomers. The greater number are single-rooted, those with divided roots being very exceptional. The crown consists chiefly of dentine, covered with a layer of enamel; cement enters but slightly into its composition, and vasodentine is entirely wanting. The form is usually sharply conical, either erect or recurved, but there are many other varieties, such as depressed, hemispherical, or even pavement-like teeth; some have bevelled edges, or are chisel- or spade-shaped, and a few are multi-cuspidate. Some have solid crowns, others grow from persistent pulps. *Thecodont* or socketed teeth are inserted in alveoli, *acrodont* teeth are fused with the supporting bone along the outer rim or top, and *pleurodont* teeth are fused laterally along the flange-like inner rim of the jaw. The successional teeth arise on the inner side of the functional teeth, and replace the latter by causing the resorption of their bases. In the Crocodiles and Placodonts replacement does not occur until the successional teeth have moved directly beneath the functional teeth.

Except in Snakes and certain Lacertilians, two pairs of limbs are always present. In the *pectoral arch* the principal bones are the coracoid and scapula, which originate in cartilage and form the glenoid cavity for the humerus. In some of the more primitive Reptiles there is also a separately ossified precoracoid. Clavicles and an interclavicle, which are membrane bones, are also often present. The scapulae are normally directed upward and backward, and are well separated by the clavicular arch when it is present. The interclavicle (or episternum) may be rhomboidal, cruciform, or T-shaped. Posterior to the interclavicle is usually a flat, rhomboidal, or shield-shaped sternum, to which the anterior dorsal ribs are attached by means of intermediate pieces. Very frequently the sternum is wanting; when present its antero-lateral margin is always applied to the coracoid, and when absent the coracoids unite in a median symphysis or are joined together by ligaments.

The appendicular skeleton (Fig. 340) is essentially as in Amphibians. In the fore limb the humerus of some primitive fossil forms is pierced at its distal end by one or two foramina, as in certain mammals; but among living reptiles this character appears only in *Sphenodon*. The ulna often exceeds the radius

in length, and is sometimes provided proximally with an olecranon process. The carpus consists always of two rows of bones, of which the proximal contains two or three, and the distal from three to six elements; occasionally these rows are separated by one or two centralia. There are commonly from two to five digits, and among Ichthyosaurs even more than five. In most Reptiles the toes comprise respectively 2, 3, 4, 5, 3 (or 4) phalanges, but the numbers are 2, 3, 3, 3, 3 in many *Theromorpha* (as in *Mammalia*), and they vary considerably in the paddles of the *Chelonia*, *Sauropterygia*, *Ichthyosauria*, and the marine *Squamata*.

Numerous modifications occur also in the pelvic region and pos-



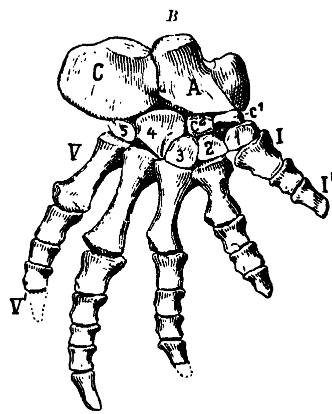


FIG. 340.

Ophiacodon mirus Marsh. *A*, Right fore limb, dorsal view; and *B*, right hind foot, dorsal view. Lower Permian; New Mexico. *A*, astragalus; *C*, calcaneum; *c*¹, *c*², centralia; *Fo*, entepicondylar foramen; *H*, humerus; *i*, intermedium; *P*, pisiform; *R*, radius; *r*, radiale; *U*, ulna; *u*, ulnare; 1-5, carpalia (tarsalia); *I-V*, metacarpalia (metatarsalia); *I*¹-*V*¹, phalanges. About 1/4 nat. size (after Williston).

terior limb. A sacrum, consisting normally of two vertebrae, is present in all Reptiles except Ichthyosaurs, Snakes, and Pythonomorphs. Among Snakes the pelvis is either entirely wanting, or represented by vestiges; and rudimentary ilia are present among apodal Lizards. All other Reptiles have a pelvis composed of the three usual elements, and as a rule they all take part in the formation of the acetabulum. The ilium is often much extended antero-posteriorly. The ischia are generally larger than the pubes, and both pairs converge ventrally in front, and join in median symphyses. The hind limb closely resembles the fore limb in most cases. One or two trochanters may occur on the proximal portion of the femur, and there are generally two rows of tarsals. The *Sauropsida* (Reptiles and Birds) differ from Mammals in having the ankle-joint between the two rows of tarsals, and never between the tibia and proximal tarsals.

Their respiration being exclusively by lungs, Reptiles are adapted to a terrestrial or amphibious life. Even the small number of marine Chelonians and Lacertilians visit the shores periodically for the purpose of depositing their eggs. Among extinct forms, Ichthyosaurs, Sauropterygians, Pythonomorphs, and many Crocodiles were truly marine, and provided with paddle-

shaped extremities. The majority of fossil Reptiles, however, were land forms; some appear to have been arboreal, and the Pterosaurs, as their name implies, were adapted for flight, or at least capable of gliding through the air.

The extinct Reptiles exhibit far greater diversity in structure than living forms, and hence a knowledge of their organisation is indispensable for an

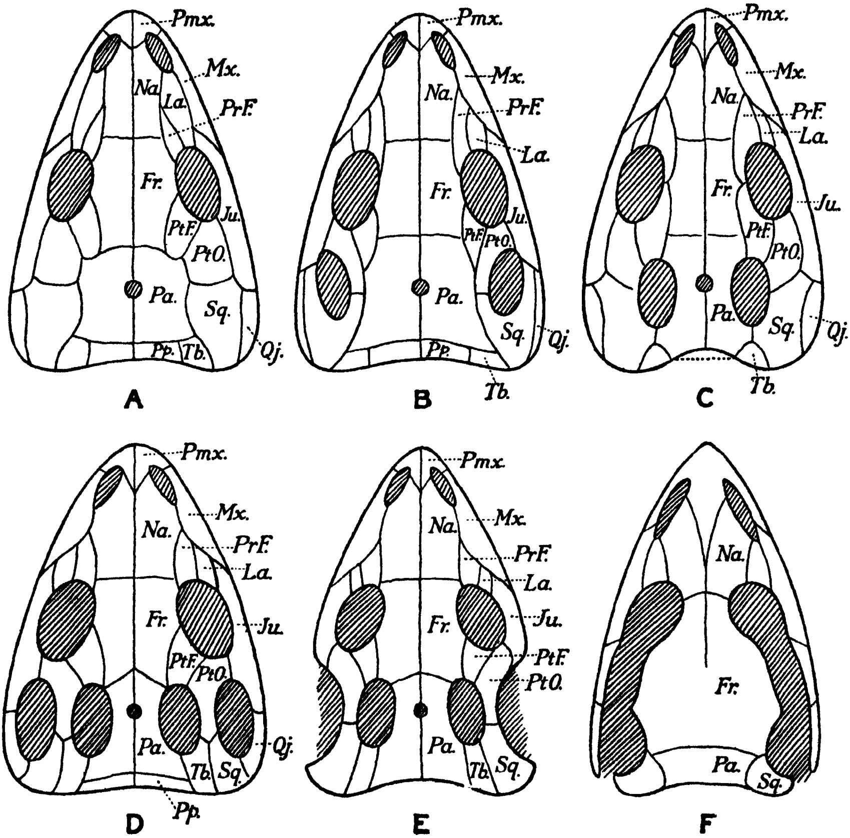


FIG. 341.

Diagram of the Cranial Roof in the various groups of Reptiles and a Bird, drawn by Dr. Robert Broom. *A*, primitive type with temporal region roofed (*Anapsida*); *B*, with lateral temporal vacuity (*Synapsida*, leading to *Mammalia*); *C*, with upper temporal vacuity (*Parapsida*); *D*, with lateral and upper temporal vacuities (*Diapsida*, derived from *Parapsida*); *E*, with lower arch which usually bounds lateral temporal vacuity missing (*Squamata*, derived from *Diapsida*); *F*, bird (derived from *Diapsida* by loss of arches between temporal vacuities and orbits). The bone marked *Tb* (tabular) in Figs. *C*, *D*, *E*, is generally described as supratemporal.

understanding of the Class. The earliest undoubted reptilian remains are of Lower Permian age, and numerous forms are known from the Permian of Europe, North America, and South Africa. The culmination of the Class occurred during the Jura-Trias, after which Reptiles steadily declined.

Reptiles and Amphibians were first distinguished and separated by Blainville in 1816 and by Merrem in 1820, but a satisfactory classification was impossible until after the researches of Owen, Huxley, von Meyer, Marsh, Cope, and others had much increased our knowledge of fossil forms. Even

now, many of the earliest Reptiles are still so imperfectly known that their classification is only provisional, but, following the lead of Cope and Baur, Osborn and Williston, it is generally agreed that the main groups can be diagnosed by reference to the arrangement of the roofing bones in the postero-lateral region of the skull.

In the *Anapsida* (Fig. 341, *A*), represented by the Order *Cotylosauria*, the roof remains continuous as in the Stegocephalians. In the *Synapsida* (Fig. 341, *B*), represented by many of the *Theromorpha*, a single temporal vacuity occurs on each side separated from the parietal by a band of bone which is formed by the postorbital and squamosal. In the *Parapsida* (Fig. 341, *C*), represented by the Orders *Araeoscelidia*, *Ichthyosauria*, *Placodontia*, and *Sauropterygia*, a single temporal vacuity occurs on each side between the parietal, postorbital, and squamosal. In the *Diapsida* or *Archosauria* (Fig. 341, *D*), both these temporal vacuities occur on each side. From the *Diapsida* appear to be derived the *Squamata* (Fig. 341, *E*), which lose the lower, and often also the upper arch of bone bounding the temporal vacuities. From the *Diapsida* likewise may be derived the Birds (Fig. 341, *F*), in which the postorbital and upper temporal arches disappear.

By Williston and Nopcsa the Order *Chelonia* is referred to the *Anapsida*, but the absence of a precoracoid and certain other characters seem to suggest its affinities with the Orders of *Parapsida*. By Williston the *Placodontia* and *Sauropterygia* are separated from the *Parapsida* as *Synaptosauria*, by Nopcsa as *Dranitesauria*. By both Williston and Nopcsa the *Squamata* are regarded as derived not from the *Diapsida*, but from the *Parapsida*.

Order 1. COTYLOSAURIA.[1]

Primitive land reptiles. Cranial roof continuous over temporal region, and bones often sculptured. A pair of narial openings, and a pineal foramen. Vertebrae amphicoelous, often pierced by notochord; neural spines low and stout. Bones of pectoral arch fused or firmly united by suture; a distinct precoracoid. Bones of pelvic arch fused or firmly united by suture, meeting in median symphysis; a pubic foramen; acetabulum not perforate. Phalangeal formula usually 2, 3, 4, 5, 3 (4). Dermal ossifications small or absent.

The Cotylosaurians, ranging from the Lower Permian to the Trias, though mostly Permian, are found in North America, Europe, and South Africa. They are a primitive group of Reptiles closely related to the Temnospondylous Stegocephalians, and, like these, seem to have lived chiefly in marshes. Their continuous cranial roof, which is often sculptured (though without slime canals), the varied development of the otic notches behind, and the frequent presence of a cleithrum, are all Stegocephalian characters. They are distinguished by the reduction of the intercentra, the low and thickened neural arches with horizontal zygapophysial facets, and the presence of only two bones in the proximal row of the tarsus.

According to D. M. S. Watson, the inclined quadrate bone of the *Stego-*

[1] *Boulenger, G. A.*, Considérations sur les reptiles permo-triasiques de l'ordre des Cotylosauriens. Comptes rendus Acad. Sci. Paris, vol. 165, p. 456, 1917.—*Case, E. C.*, Revision of the Cotylosauria of North America. Public. Carnegie Inst. Washington, no. 145, 1911.—*Watson, D. M. S.*, Brain-case in certain Lower Permian Tetrapods. Bull. Amer. Mus. Nat. Hist., vol. xxxv., p. 611, 1916. See also Bibliography of *Theromorpha*, p. 247.

cephali has become vertical in the *Cotylosauria* in two different ways. In the *Pareiasauria* the lower end of the bone has advanced forwards, in the *Labidosauria* the upper end has moved backwards.

Sub-Order 1. PAREIASAURIA.

Head relatively large, with vertical quadrate and exaggerated laterally placed auditory (otic) notches. Tabular bones extended on dorsal surface. Septomaxillary bone present.

Family 1. Pareiasauridae.[1]

Brain-case long and low; ear-cavity separated by bone from brain-cavity; tabulars and postparietals only on dorsal surface; large post-temporal fossae; one

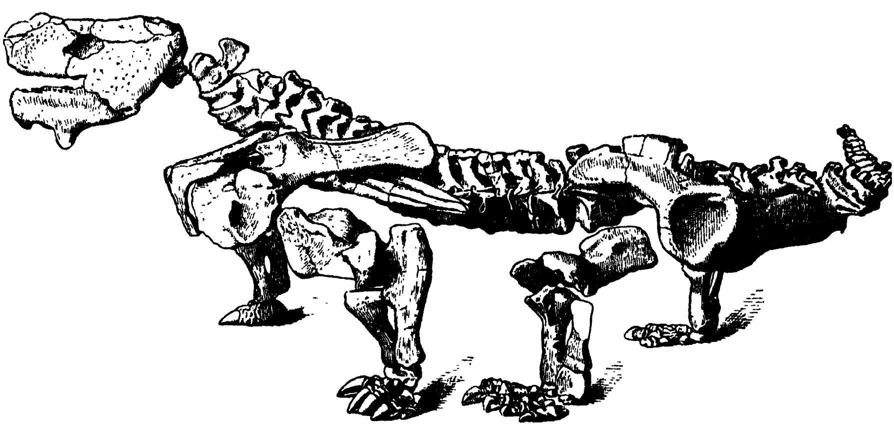


Fig. 342.

Pareiasaurus (Bradysaurus) baini Seeley. Karroo Formation (Permian); Tamboer Fontein, Cape Colony. Skeleton; $^1/_{20}$ nat. size (after Seeley).

occipital condyle. Teeth conical, or with compressed, cuspidate crown, those on the margin of the jaws arranged in a close regular series. Smaller teeth usually present on palatines, pterygoids, and vomers. Pelvic bones fused in the adult. Limbs short and stout. Permian.

Pareiasaurus Owen (*Bradysaurus* Watson; *Bradysuchus, Nochelesaurus, Dolichopareia, Koalemasaurus, Brachypareia, Platyoropha* Haughton and Boonstra) (Figs. 342, 343). Skull broad, depressed, and triangular in form, the

[1] *Boonstra, L. D.*, Pareiasaurian Manus. Ann. S. African Mus., vol. xxxviii., p. 97, 1929; also Pareiasaurian Pes. *Loc. cit.*, p. 113, 1929.—Cranial Osteology of *Pareiasaurus serridens* (Owen). Ann. Univ. Stellenbosch, vol. viii., sect. A, no. 5, 1930.—*Broom, R.*, Skeleton of *Pareiasaurus serridens.* Ann. S. African Mus., vol. iv., p. 123, 1903.—Pareiasaurian genus *Propappus. Loc. cit.*, vol. iv., p. 351, 1908.—New Species of *Propappus* and Pose of Pareiasaurian Limb. *Loc. cit.*, vol. vii., p. 323, 1912.—*Broom, R.*, and *Haughton, S. H.*, Skeleton of new Pareiasaurian (*Pareiasuchus peringueyi*). *Loc. cit.*, vol. xii., p. 17, 1913.—*Hartmann-Weinberg, A.*, Carpus und Tarsus der Pariasauriden. Anat. Anzeig., vol. lxvii., p. 401, 1929.—Zur Systematik der Nord-Düna-Pareiasauridae. Palaeont. Zeitschr., vol. xii., p. 47, 1930.—*Haughton, S. H.*, Some Pareiasaurian Brain-Cases. Ann. S. African Mus., vol. xxviii., p. 88, 1929.—*Haughton, S. H.*, and *Boonstra, L. D.*, Classification of the *Pareiasauria. Loc. cit.*, vol. xxviii., p. 79, 1929.—Pareiasaurian Mandible. *Tom. cit.*, p. 261, 1930.—Hind Limb. *Tom. cit.*, pp. 297, 429, 1930-32.—Fore

external bones coarsely sculptured, but their sutures not clearly distinguishable. Orbits relatively small, laterally placed. Occipital condyle slightly indented. Bones of the palate fused, and bearing several series of small teeth. Stapes articulating with quadrate. About eighteen presacral vertebrae, each with a deepened articulation for the ribs, which are only double-headed anteriorly. Small intercentra between all the dorsal vertebrae; the four sacrals not fused. About thirty caudal vertebrae, the anterior with short ribs, and nearly all with neural arches and chevron bones. Scapula very long, with acromial process. Coracoid small and subrectangular, precoracoid narrow and triangular; clavicles robust, meeting in the middle line and resting on the front border of the large T-shaped interclavicle. A cleithrum also present on each side. Glenoid cavity screw-shaped. Humerus short, massive, expanded at the ends; an entepicondylar foramen. Ulna very stout with prominent olecranon process. Pelvic bones massive, coössified. Hind limb slightly shorter than the fore limb, and digits smaller; the five digits of both feet with broad claws. Body with several rows of bony dermal scutes. *P. serridens*, *P. bombifrons* Owen; *P. baini* Seeley. Skeletons from 2 m. to 3 m. long from Karroo Formation (Lower Beaufort Beds, *Tapinocephalus* Zone), S. Africa. Phalangeal formula of fore foot, 2, 3, 3, 3, 2. According to Haughton and Boonstra, who propose to distribute the species of *Pareiasaurus* in several genera, the earliest Pareiasaurs have the marginal teeth with high crowns and few cusps, while the later forms have teeth with low and broad crowns and numerous cusps.

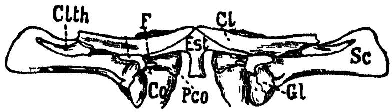


FIG. 343.

Pareiasaurus (*Bradysaurus*) *baini* Seeley. Restoration of pectoral arch. Permian; South Africa. *Cl*, clavicle; *Clth*, cleithrum; *Co*, coracoid; *Est*, interclavicle; *F*, supracoracoid foramen; *Gl*, glenoid facet for humerus; *Pco*, precoracoid; *Sc*, scapula. Much reduced (after Seeley and Furbringer).

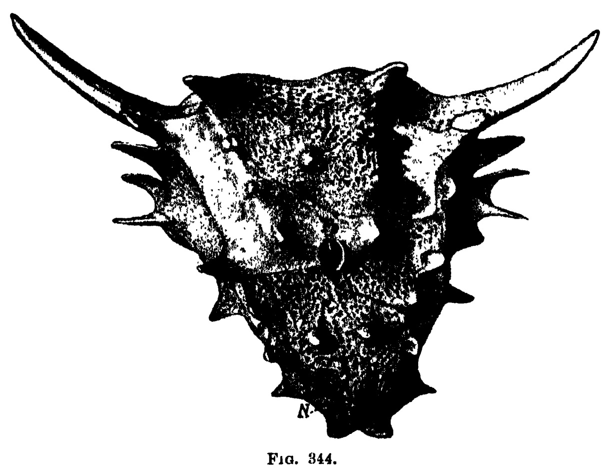


FIG. 344.

Elginia mirabilis Newton. Skull, from above. Permian; Elgin, Scotland. *Fp*, pineal foramen; *N*, external narial opening; *O*, orbit. $^1/_3$ nat. size (after E. T. Newton).

Pareiasuchus Broom and Haughton. Differing from *Pareiasaurus* in the large quadrato-jugal region inclined far outwards and forwards so that its

Limb. *Tom. cit.*, p. 437, 1932.—*Newton, E. T.*, New Reptiles from the Elgin Sandstones. Phil. Trans. Roy. Soc., vol. 184B, p. 473 [*Elginia*], 1893.—*Seeley, H. G.*, *Pareiasaurus bombidens.* Phil. Trans. Roy. Soc., vol. 179B, p. 59, 1888.—Further Observations on *Pareiasaurus. Loc. cit.*, vol. 183B, p. 311, 1892.—Armour of *Pareiasaurus.* Proc. Zool. Soc., 1908, p. 605.—*Sushkin, P. P.* [Skull of "*Pareiasaurus*" *karpinskii*]. Palaeont. Zeitschr., vol. viii., p. 293, 1927.—*Watson, D. M. S.*, Skull of a Pariasaurian Reptile. Proc. Zool. Soc., 1914, p. 155.—Nomenclature of South African Pariasaurians. Ann. Mag. Nat. Hist. [8], vol. xiv., p. 98, 1914.

lower border makes an angle of about 120° with the maxillary border; this cheek bearing large bony bosses. *P. peringueyi* B. and H., known by nearly complete skeleton from Lower Beaufort Beds, Zak River, S. Africa. *P. karpinskii* Sushkin, known by skeletons 2 m. to 3 m. long from Permian, Northern Dwina, Russia (well armoured and referred to a distinct genus *Scutosaurus* by Hartmann-Weinberg).

Anthodon Owen. Karroo Formation; S. Africa.

Embrithosaurus Watson. Bony dermal scutes thin and smooth. Ulna without olecranon process. Lowest Beaufort Beds; S. Africa.

Propappus Seeley. Back thickly covered with large, slightly sculptured bony scutes. No ventral armour observed. Lower Beaufort Beds; S. Africa.

Elginia Newton (Fig. 344). Known only by the skull, which is about 15 cm. long, triangular, coarsely sculptured, and provided with a number of paired bosses and spinous or horn-like defences. These occur along the posterior and lateral margins, and on the parietal, frontal, and nasal bones. Teeth with slightly constricted base and serrated crown. Permian of Elgin, Scotland.

Family 2. **Diadectidae.**[1]

Brain-case long and low; ear-cavity not separated by bone from brain-cavity. Lachrymal bone reaching nostril; no post-temporal fossae. Anterior teeth obtusely conical, the other marginal teeth transversely extended, with tumid bases and inner and outer cusps of unequal height. Vomer with minute teeth. Cleithrum present. Permian.

Diadectes Cope (*Empedias* Cope; ? *Nothodon* Marsh). Skull about 20 cm. long, with sculptured ornament. Orbits small and lateral; pineal foramen

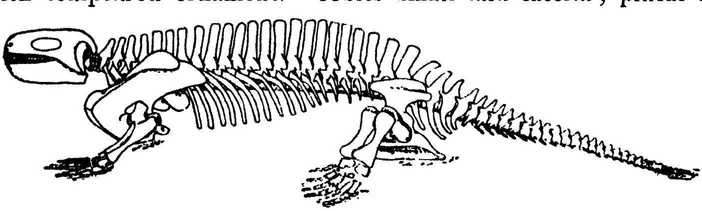


FIG. 345.

Diasparactus zenos Case and Williston. Restoration of skeleton. Lower Permian; New Mexico. About $^1/_{16}$ nat. size (after Case and Williston).

very large; large lateral otic notch. Interclavicle T-shaped. Cleithrum fused with front edge of scapula. Over twenty presacral vertebrae, with hyposphene and hypantrum articulation; two sacrals, and over thirty caudals. Intercentra present. Phalangeal formula of hind foot, 2, 3, 4, 5, 4. *D. sideropelicus* Cope. Lower Permian; Texas, U.S.A. Other species in New Mexico and Oklahoma.

Diadectoides Case. With one sacral vertebra. Lower Permian; Texas.

[1] *Broom, R.*, Diadectid Skull. Bull. Amer. Mus. Nat. Hist., vol. xxxiii., p. 109, 1914.—*Case, E. C.*, Osteology of the Diadectidae. Journ. Geol., vol. xiii., p. 126, 1905.—Restoration of *Diadectes*. *Loc. cit.*, vol. xv., p. 556, 1907.—New or little-known Reptiles and Amphibians from the Permian (?) of Texas. Bull. Amer. Mus. Nat. Hist., vol. xxviii., p. 163, 1910.—*Case, E. C.*, and *Williston, S. W.*, Skulls of *Diadectes lentus* and *Animasaurus carinatus*. Amer. Journ. Sci., vol. xxxiii., p. 339, 1912.—*Romer, A. S.*, Permian Amphibian and Reptilian Remains described as *Stephanospondylus*. Journ. Geol., vol. xxxiii., p. 447, 1925.

Diasparactus Case (Fig. 345). *Animasaurus* Case and Williston. Permian; New Mexico.

Desmatodon Case. Permian; Pennsylvania.

Stephanospondylus Stappenbeck. Molar teeth without lateral cusps. Vertebrae without hyposphene-hypantrum articulation. Cleithrum very large. *S. pugnax* Geinitz and Deichmüller sp., about one metre long. Middle Rothliegendes; Dresden.

? *Phanerosaurus* H. von Meyer. Permian; Saxony.

Chilonyx, *Bolbodon* Cope. Permian; Texas.

Family 3. Procolophonidae.[1]

Brain-case short and high; ear-cavity not separated by bone from brain-cavity; lachrymal bone short, not reaching nostril; tabular bone large, partly extended on

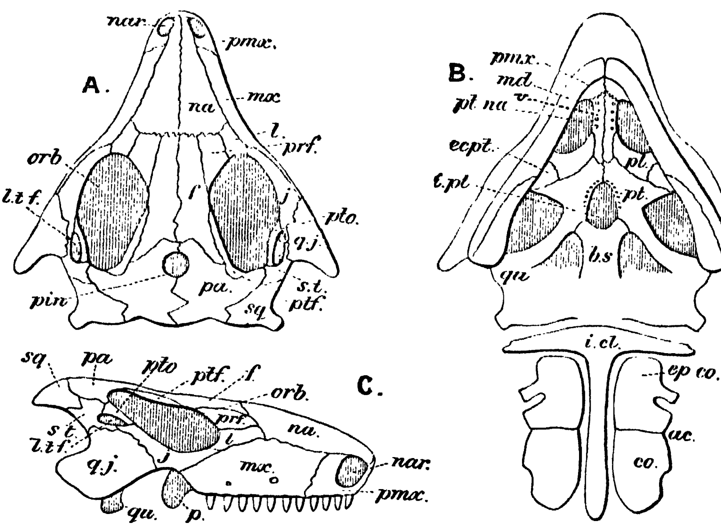


FIG. 346.

Procolophon trigoniceps Owen. Karroo Formation (Upper Beaufort Beds); South Africa. Restoration of skull from superior (*A*), inferior (*B*), and lateral (*C*) aspects, also part of the pectoral arch, slightly reduced. *ac*, glenoid cavity for humerus; *bs*, basisphenoid; *co*, coracoid; *ecpt*, ectopterygoid; *epco*, precoracoid (epicoracoid); *f*, frontal; *icl*, interclavicle; *ipt*, interpterygoid vacuity; *j*, jugal; *l*, lachrymal; *ltf*, accidental vacuity; *md*, mandible; *mx*, maxilla; *na*, nasal; *nar*, external nares; *orb*, orbit; *p*, downward ectopterygoid process; *pa*, parietal; *pin*, pineal foramen; *pl*, palatine; *pmx*, premaxilla; *prf*, prefrontal; *pt*, pterygoid; *ptna*, internal nares; *ptf*, postfrontal; *pto*, postorbital; *qj*, quadrato-jugal; *qu*, quadrate; *st*, squamosal; *sq*, tabular; *v*, vomer (after A. S. Woodward).

occipital surface; large post-temporal fossae. Marginal teeth transversely extended; a few small conical teeth on palate. No cleithrum. Triassic.

Procolophon Owen (Fig. 346), Skull short and triangular, not externally

[1] *Boulenger, G. A.*, The Triassic Reptile *Telerpeton elginense*. Proc. Zool. Soc., 1904, vol. i., p. 470.—*Gilmore, C. W.*, New Fossil Reptile from the Triassic of New Jersey. Proc. U.S. Nat. Mus., vol. lxxiii., art. 7, 1928.—*Huene, F. von*, Die Procolophoniden. Centralbl. f. Min., etc., 1911, p. 78.—Ein *Telerpeton* mit gut erhaltenem Schädel. *Loc. cit.*, 1920, p. 189.—*Sclerosaurus*. Zeitschr. f. indukt. Abstammungs- u. Vererbungslehre, vol. xxiv., p. 163, 1920.—*Seeley, H. G.*, *Aristodesmus ruetimeyeri* (Wiedersheim). Quart. Journ. Geol. Soc., vol. lvi., p. 620, 1900.—*Procolophon*. Proc. Zool. Soc., 1905, vol. i., p. 218.—*Watson, D. M. S.*, *Procolophon trigoniceps*. Proc. Zool. Soc., 1914, p. 735.

sculptured. Orbits and pineal foramen greatly enlarged. A single row of minute teeth on each vomer and pterygoid. Stapes not articulating with quadrate; twenty-six presacral, three sacral vertebrae. Interclavicle T-shaped, with elongated arms; precoracoid notched. Abdominal ribs present, but reduced. *P. trigoniceps* Owen, with skeleton about 30 cm. long, skull 5 cm. long. Karroo Formation (Upper Beaufort Beds); South Africa.

Telerpeton Mantell (*Leptopleuron* Owen). Much resembling *Procolophon*, but molariform teeth wider, no abdominal ribs, and hind limb more slender. *T. elginense* Mant. Triassic; Elgin, Scotland.

Thelegnathus Broom. Karroo Formation (Upper Beaufort Beds); South Africa.

Sclerosaurus H. von Meyer (*Aristodesmus* Seeley). With spines on head, and six longitudinal rows of bony plates on back. *S. armatus* H. v. Mey. Upper Bunter Sandstone; Riehen, near Basle, Switzerland.

Koiloskiasaurus v. Huene. U. Bunter Sandstone; Coburg.

Trilophosaurus Case. U. Triassic; W. Texas, U.S.A.

? *Hypsognathus* Gilmore. U. Triassic; New Jersey, U.S.A.

Sub-Order 2. LABIDOSAURIA.

Head relatively large, with vertical quadrate and auditory (otic) notches obliterated. Tabular bones extended on occipital surface, or absent.

Family 1. Captorhinidae.[1]

Frontals bordering orbit. Premaxillary teeth enlarged and recurved. Vertebrae elongated. Limb bones slender. Lower Permian.

Captorhinus Cope (*Hypopnous, Ectocynodon* Cope). Skull about 6 cm. long, with very small pineal foramen. Two to four rows of teeth on maxilla;

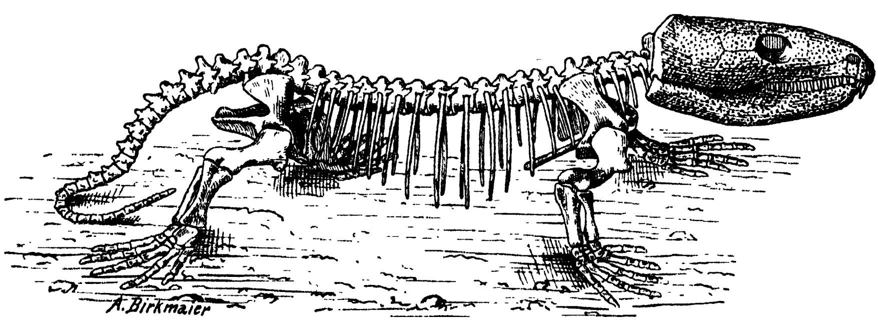


FIG. 347.
Labidosaurus hamatus Cope. Restoration of skeleton. Permian; Texas. From mounted skeleton in the Palaeontological Museum, Munich, about $^1/_5$ nat. size.

minute teeth on pterygoid. Large postarticular process in mandible. Intercentra present; two sacral vertebrae. Phalangeal formula of hind foot

[1] *Branson, E. B.*, Skull of *Pariotichus*. Journ. Geol., vol. xix., p. 135, 1911.—*Broili, F.*, Skelett von *Labidosaurus hamatus* Cope. Zeitschr. Deutsch. Geol. Ges., vol. lx., p. 63, 1908.—*Case, E. C.*, *Pariotichus incisivus* Cope. Zool. Bull., vol. ii., p. 231, 1899.—*Sushkin, P. P.*, Cranial Morphology of *Captorhinus* Cope. Palaeobiologica, vol. i., p. 263, 1928.—*Williston, S. W.*, *Pariotichus*. Biol. Bull., vol. xvii., p. 241, 1909.—Skull of *Labidosaurus*. Amer. Journ. Anat., vol. x., p. 69, 1910.—*Labidosaurus* Cope. Journ. Geol., vol. xxv., p. 309, 1917.

probably 2, 3, 4, 5, 4. *C. aguti* and *isolomus* Cope. Lower Permian; Texas, U.S.A.

Labidosaurus Cope (Figs. 347-349). Skeleton about 70 cm. long. Skull sculptured, with grasping premaxillae. According to Broili the supposed

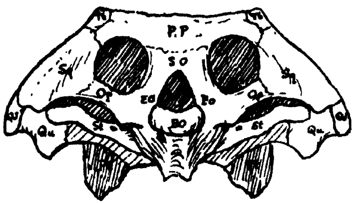


FIG. 348.

Labidosaurus hamatus Cope. Back view of skull. Permian; Texas. *Bo*, basioccipital; *Eo*, exoccipital; *Op*, opisthotic; *PP*, postparietal; *Pt*, pterygoid; *Qu*, quadrate; *Qj*, quadratojugal; *So*, supraoccipital; *Sq*, squamosal; *St*, stapes; *Tb*, tabular. 1/2 nat. size (drawn by Dr. R. Broom).

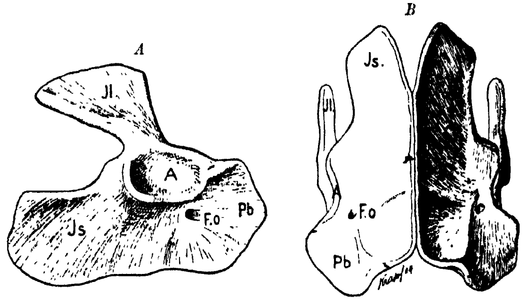


FIG. 349.

Labidosaurus hamatus Cope. Pelvis in right outer view (*A*) and from below (*B*). Permian; Texas. *A*, acetabulum; *Fo*, obturator foramen; *Jl*, ilium; *Js*, ischium; *Pb*, pubis. About 1/2 nat. size (after Broili).

labyrinthodont folds in the dentine of the teeth, which he originally described, are due to post-mortem splitting. One row of teeth on maxilla; no post-articular process in mandible. Intercentra present; about twenty-five presacral, two sacral, and twenty-five caudal vertebrae. No cleithrum. *L. hamatus* Cope. Lower Permian; Texas.

? *Pariotichus, Helodectes, Isodectes* Cope. Lower Permian; Texas.

Family 2. **Limnoscelidae.**[1]

Frontals excluded from orbit. Premaxillary teeth enlarged. Vertebrae short. Ends of limb bones expanded. Carpus and tarsus incompletely ossified. Lower Permian.

Limnoscelis Williston. Skeleton about 2 m. long. Cranial roof flattened and smooth; pineal foramen small; snout laterally compressed. Conical teeth in single row on edge of jaw. Twenty-six presacral, one sacral, and one sacrocaudal vertebrae. Intercentra present. Cleithrum small. Phalangeal formula of hind foot, 2, 3, 4, 5, 4. *L. paludis* Williston. Lower Permian; New Mexico, U.S.A.

Sub-Order 3. PANTYLOIDEA.

Head large, with vertical quadrate and auditory (otic) notches obliterated. Tabular bones extended on dorsal surface.

Family **Pantylidae.**[2]

Maxilla, palate, and mandible with numerous teeth. Lower Permian.

Pantylus Cope (*Ostodolepis* Williston). Head bones sculptured; pineal foramen not observed. Teeth blunt. Small dermal ossifications. Texas.

[1] *Williston, S. W.*, New Family of Reptiles from the Permian of New Mexico. Amer. Journ. Sci., vol. xxxi., p. 378, 1911.—Restoration of *Limnoscelis*. *Loc. cit.*, vol. xxxiv., p. 457, 1912.

[2] *Broom, R.*, Cotylosaurian genus *Pantylus*. Bull. Amer. Mus. Nat. Hist., vol. xxxii., p. 527, 1913.—*Case, E. C.*, Nearly complete Skeleton of *Ostodolepis*. Contrib. Mus. Palaeont. Univ. Michigan, vol. iii., p. 81, 1930.—*Williston, S. W.*, *Pantylus*. Contrib. Walker Mus., Chicago, vol. i., p. 165, 1916.

Sub-Order 4. EUNOTOSAURIA.

Head comparatively small and neck slender. Dorsal vertebrae long and slender; ribs arched and much expanded.

The systematic position of the *Eunotosauria* is uncertain, but their pectoral and pelvic arches most closely resemble those of the *Cotylosauria*. They are regarded by Watson as possibly ancestral *Chelonia*.

Family **Eunotosauridae**.[1]

Teeth on palate. Trunk short and broad, with a dorsal dermal armour; rib facets far forward on the centra. Permian.

Eunotosaurus Seeley. Ten dorsal vertebrae. *E. africanus* Seeley, from Karroo Formation (Lower Beaufort Beds), Beaufort West, Cape Colony, about 20 cm. in length to base of tail.

Order 2. THEROMORPHA.[2]

(*Anomodontia* Owen, *Theromora* Cope.)

Primitive land reptiles with limbs usually adapted for habitual support of the body. Roofing bones of the temporal region of the skull contracting into a single broad arch (squamoso-jugal or squamoso-postorbital); auditory region low down on side of brain-case; quadrate usually firmly fixed; usually a pineal foramen; septomaxillary bone in narial opening. Teeth on margin of jaws in sockets; sometimes teeth on palate. Vertebrae amphicoelous, often pierced by notochord; ribs at least in part double-headed, articulating with arches as well as centra. Sacrum of two to six vertebrae. Bones of pectoral arch fused or firmly united by suture; a distinct precoracoid. Humerus with entepicondylar foramen. Bones of pelvic arch fused or firmly united by suture, meeting in median symphysis; pubis and ischium plate-like, the pubis pierced by a foramen; acetabulum not perforate. Feet five-toed. Dermal ossifications usually absent.

The *Theromorpha* were thus named by E. D. Cope in allusion to the many resemblances in their skeleton to that of the Mammals, especially the *Monotremata*. Their pelvic bones are fused into an *os innominatum* as in Mammals; their pectoral arch is remarkably like that of the Monotreme Mammals; and

[1] *Seeley, H. G.*, New Reptile *Eunotosaurus africanus* (Seeley). Quart. Journ. Geol. Soc., vol. xlviii., p. 583, 1892.—*Watson, D. M. S.*, *Eunotosaurus africanus* Seeley, and the Ancestry of the Chelonia. Proc. Zool. Soc., 1914, p. 1011.

[2] *Broom, R.*, Comparison of the Permian Reptiles of North America with those of South Africa. Bull. Amer. Mus. Nat. Hist., vol. xxviii., p. 197, 1910.—Origin of Mammals. Phil. Trans. Roy. Soc., vol. 206 B, p. 1, 1914.—Permian, Triassic, and Jurassic Reptiles of South Africa. Bull. Amer. Mus. Nat. Hist., vol. xxv., p. 105, 1915.—The Mammal-like Reptiles of South Africa. London, 1932.—*Haughton, S. H.*, Brain-case in certain *Therapsida*. Ann. S. African Mus., vol. xii., p. 202, 1918.—Review of the Reptilian Fauna of the Karroo System. Trans. Geol. Soc. S. Africa, vol. xxii., p. 1, 1919.—Bibliographic List of Pre-Stormberg Karroo Reptilia. Trans. Roy. Soc. S. Africa, vol. xii., p. 51, 1925.—Palaeontology in South Africa. Proc. Geol. Soc. S. Africa, 1926, p. xx.—*Huene, F. von*, Fauna der südafrikanischen Karrooformation [especially *Dinocephalia* and *Anomodontia*]. Geol. u. Palaeont. Abhandl., n.f., vol. xviii., p. 159, 1931.—*Romer, A. S.*, Vertebrate Faunal Horizons in the Texas Permo-Carboniferous Red Beds. Univ. Texas Bull., 2801, p. 67, 1928. Most of these papers also refer to the *Cotylosauria*.

the latest members of the Order, the *Cynodontia*, have the marginal teeth differentiated into incisors, canines, premolars, and molars, while their lower jaw consists mainly of the dentary bones with the hinder bones extremely reduced. Through the *Cotylosauria* the *Theromorpha* are closely connected with the *Stegocephali*. In their skeleton, therefore, they are intermediate between the early *Amphibia* and the lowest known *Mammalia*.

The *Theromorpha* are an extremely varied group of Reptiles, and had a wide geographical distribution. Their remains are especially abundant in the Karroo Formation (Permo-Triassic) of South Africa, and are also found in corresponding rocks in India, northern Russia, central Europe, northern Scotland, the United States of North America, and southern Brazil.

The *Dinocephalia*, *Dromasauria*, *Dicynodontia*, and *Theriodontia* are grouped by Broom as *Therapsida*.

Sub-Order 1. PELYCOSAURIA.[1]

Occipital condyle single but tripartite, formed by basioccipital and exoccipitals; quadrate bone small; no secondary palate. Marginal teeth conical, usually laterally compressed, the cutting edges often serrated; some anterior upper teeth relatively large; palatal teeth relatively small. Vertebrae notochordal, with intercentra in all precaudals; a proatlas: two or three sacral vertebrae. Coracoid and precoracoid not fused with scapula until old age; scapula without acromion; interclavicle T*-shaped or with rhombic expansion; a rudimentary cleithrum. Phalangeal formula probably 2, 3, 4, 5, 3 (4).*

Family 1. **Palaeohatteriidae.**[2]

Skull laterally compressed, with very large lachrymal reaching external narial opening on each side; tooth-bearing border of maxilla straight. Neural spines of vertebrae short. Limbs very slender; the humerus not much expanded at lower end. Abdominal scutes present. Lower Permian.

Palaeohatteria Credner (Fig. 350). Long-tailed and lizard-shaped. Snout short and bluntly pointed; orbit very large, with ring of sclerotic plates. Teeth nearly uniform, but two slightly enlarged in middle of maxilla; smaller teeth on palate. About six cervical, twenty trunk, three sacral, and fifty caudal vertebrae; the intercentra continuing as far back as the sixth caudal. Interclavicle with rhombic expansion at anterior end. Pubis with obturator notch. Hind limb slightly longer than fore limb. Numerous oat-shaped scutes representing abdominal ribs. *P. longicaudata* Credner, about 45 cm. long. Lower Permian (Middle Rothliegendes); Niederhässlich, near Dresden.

[1] *Case, E. C.*, Revision of the Pelycosauria of North America. Public. Carnegie Inst. Washington, no. 55, 1907.—Inner Ear in two primitive Reptiles. Biol. Bull., vol. xxvii., p. 213, 1914.—*Huene, F. von*, Neue und verkannte Pelycosaurier-Reste aus Europa. Centralbl. f. Min., etc., 1908, p. 431.—Pelycosaurier im deutschen Muschelkalk. Neues Jahrb. f. Min., etc., Beil.-Bd. xx., p. 321, 1905.—*Watson, D. M. S.*, Reconstructions of Skulls of three Pelycosaurs in the Amer. Mus. Nat. Hist. Bull. Amer. Mus. Nat. Hist., vol. xxxv., p. 637, 1916.

[2] *Credner, H.*, *Palaeohatteria longicaudata* Cred. Zeitschr. Deutsch. Geol. Ges., 1888, p. 490.—*Nopcsa, F.*, Redescription of *Palaeohatteria*. Geologica Hungarica, Ser. Palaeontologica, vol. i., p. 4, 1928.—*Williston, S. W.*, Osteology of some American Permian Vertebrates. Journ. Geol., vol. xxii., p. 396, 1914.

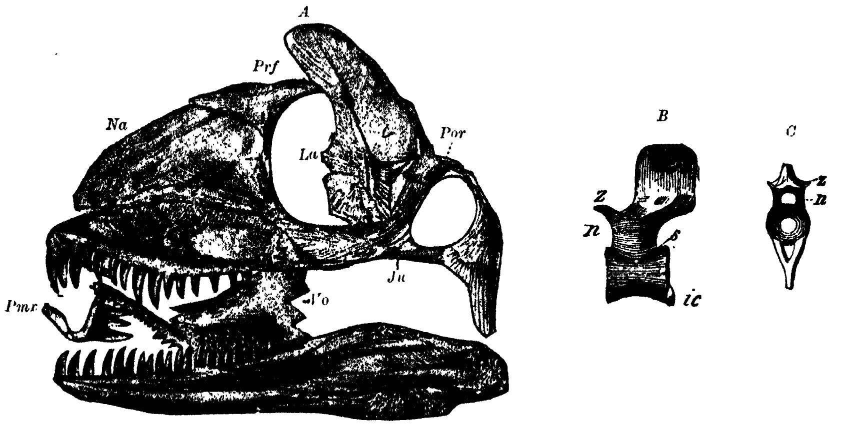


FIG. 350.
Palaeohatteria longicaudata Credner. Lower Permian; Saxony. *A*, Skull, somewhat distorted. *B*, Dorsal vertebra. *C*, Caudal vertebra, anterior aspect. *ic*, intercentrum; *Ju*, jugal; *La*, frontal; *n*, pedicle of neural arch; *Na*, lachrymal; *Pmx*, premaxilla; *Por*, postorbital; *Prf*, prefrontal; *s*, suture; *Vo*, vomer (displaced); *z*, zygapophysis. Orbit overlaid by displaced frontal bone of the right side. Nat. size (after Credner).

Family 2. **Poliosauridae**.[1]

Skull low and flat, with pointed snout; tooth-bearing border of maxilla straight, and diastemal notch small or absent. Two sacral vertebrae. All neural spines short. Abdominal ribs present. Lower Permian.

Poliosaurus Case. No well-defined canine in maxilla. *P. uniformis* Cope sp., about 70 cm. long. Texas.

Varanosaurus Broili (Fig. 351). Skull slightly sculptured; lachrymal very large, reaching external narial opening; interparietal bone present; two canines in maxilla. Twenty-seven presacral vertebrae. Dermal scutes both

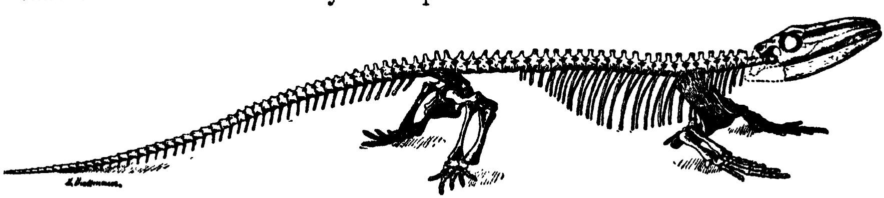


FIG. 351.
Varanosaurus acutirostris Broili. Restoration of skeleton. Lower Permian; Texas. From mounted skeleton about 1 m. long in the Palaeontological Museum, Munich.

on abdomen and on lower side of limbs. *V. acutirostris* Broili, nearly 1 m. long. Texas.

Eumatthevia Broom. Postparietal and tabular bones on occiput. Texas.

Varanops, Mycterosaurus, Glaucosaurus Williston; *Poecilospondylus* Case. Texas.

[1] *Boule, M.*, and *Glangeaud, P.*, *Callibrachion gaudryi*. Bull. Soc. Hist. Nat. Autun, vol. vi., p. 199, 1893.—*Broili, F.*, Schädelbau von *Varanosaurus*. Centralbl. f. Min., etc., 1914, p. 26.—*Case, E. C.*, Skeleton of *Poecilospondylus francisci*. Bull. Amer. Mus. Nat. Hist., vol. xxviii., p. 183, 1910.—*Thevenin, A.*, *Haptodus*, etc. Ann. Paléont., vol. v., p. 48, 1910.—*Watson, D. M. S.*, *Varanosaurus acutirostris* Broili. Ann. Mag. Nat. Hist. [8], vol. xiii., p. 297, 1914.—*Williston, S. W.*, *Mycterosaurus longiceps*. Journ. Geol., vol. xxiii., p. 554, 1915.

Anningia Broom. Preparietal bone surrounding pineal foramen. Karroo Formation (Lower Beaufort Beds); S. Africa. ? *Galesphyrus* Broom.

? *Arribasaurus* Williston; *Scoliomus* Williston and Case. New Mexico.

Haptodus Gaudry; *Callibrachion* Boule and Glangeaud. Autun, France.

Family 3. **Ophiacodontidae.**[1]

As Poliosauridae, *but skull long, high, and narrow, with small orbit far back, and tooth-bearing border of maxilla curved and teeth less uniform.* Lower Permian.

Ophiacodon Marsh (Fig. 340). Teeth slender and recurved, about thirty-six in maxilla, one in anterior half enlarged. *O. grandis* Marsh, about 1·6 m. long. New Mexico.

Theropleura Cope (*Diopaeus* Cope); *Therosaurus* F. von Huene. Texas. *Winfieldia* Romer. Kansas.

Family 4. **Pantelosauridae.**[2]

Skull short, high, and laterally compressed, with tooth-bearing border of maxilla curved, teeth irregular in size and a slight diastema. Three sacral vertebrae. All neural spines short. Lower Permian.

Pantelosaurus F. von Huene. Temporal region of skull very short; lachrymal very large, probably reaching external narial opening. About eighteen teeth in maxilla. *P. saxonicus* F. von Huene, about 1 m. long. Lower Rothliegendes; near Dresden.

Stereorhachis Gaudry. Autun, France.

Family 5. **Caseidae.**[3]

Skull short, high, and broad, with tooth-bearing border of maxilla straight, the teeth few and stout, and no diastema. Length of neural spines not greater than depth of vertebral centra. Three sacral vertebrae. Lower Permian.

Casea Williston. Pineal foramen, orbits, and narial openings remarkably large; head bones rugose; eleven teeth in maxilla and premaxilla; palate covered closely with small conical teeth. Twenty-five presacral vertebrae. Fore limb relatively long and stout. Ilium expanded in advance of acetabulum. No abdominal ribs observed. *C. broilii* Williston, about 1 m. long. Texas.

Trichasaurus Williston (*Trispondylus* Williston). Texas.

Family 6. **Clepsydropsidae.**[4]

Skull long, high, and laterally compressed, with tooth-bearing border of maxilla curved, the teeth laterally compressed and often serrated, irregular in size, with a

[1] *Romer, A. S.*, Ophiacodont Reptile from the Permian of Kansas. Journ. Geol., vol. xxxiii., p. 173, 1925.—*Williston, S. W.*, *Theropleura*. Contrib. Walker Mus. Univ. Chicago, vol. i., p. 178, 1916.—*Williston, S. W.*, and *Case, E. C.*, Nearly complete Skeleton of *Ophiacodon* Marsh. In Public. Carnegie Inst. Washington, no. 181, p. 37, 1913.

[2] *Huene F. von*, Ein neuer Pelycosaurier aus der unteren Permformation Sachsens. Geol. u. Palaeont. Abhandl., n.s., vol. xiv., p. 215, 1925.

[3] *Williston, S. W.*, Skull of *Casea*. Journ. Geol., vol. xxii., p. 403, 1914.

[4] *Broili, F.*, Pelycosaurier-reste von Texas. Zeitschr. Deutsch. Geol. Ges., vol. lvi., p. 268, 1904 [teeth of *Dimetrodon*].—*Case, E. C.*, Skeleton of *Dimetrodon incisivus*. Bull. Amer. Mus. Nat. Hist., vol. xxviii., p. 189, 1910; also Amer. Journ. Sci., vol. xl., p. 474, 1915.—*Gilmore*,

diastema. Neural spines very long, forming a crest along the back. Three sacral vertebrae. Lower Permian to Lower Triassic.

Clepsydrops Cope. Lachrymal bone short. Diastema between maxilla and premaxilla filled by small teeth. One or two relatively large teeth at

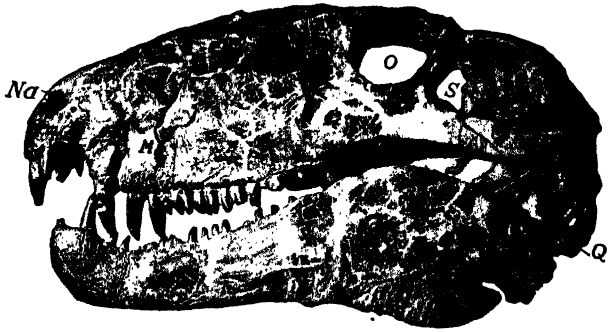


FIG. 352.
Dimetrodon incisivus Cope. Skull and mandible in left side view. Permian; Texas. *M*, maxilla; *Na*, external narial opening; *O*, orbit; *Pm*, premaxilla; *Q*, quadrate; *S*, temporal vacuity. 1/5 nat. size (after Case).

front end of maxilla, which bears about twenty teeth. Neural spines simple, vertical, slightly recurved in lumbar region. Articular ends of limb bones imperfectly ossified. *C. colletti* Cope, about 1 m. long. Illinois and Texas.

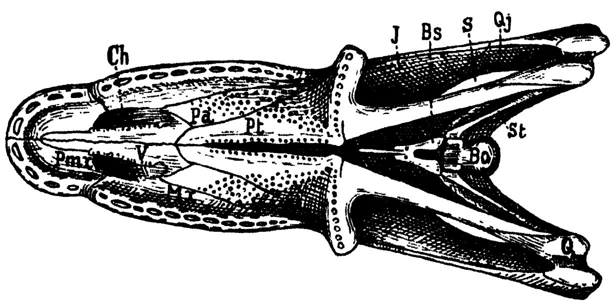


FIG. 353.
Dimetrodon gigas Cope. Restoration of skull from below. Permian; Texas. *Bo*, basioccipital; *Bs*, basisphenoid; *Ch*, internal narial opening; *J*, jugal; *Mx*, maxilla; *Pa*, palatine; *Pmx*, premaxilla; *Pt*, pterygoid; *Q*, quadrate; *Qj*, quadrato-jugal; *S*, temporal vacuity; *St*, stapes; *V*, vomer. 1/6 nat. size (after Case).

Sphenacodon Marsh. New Mexico.

Dimetrodon Cope (*Embolophorus* Cope) (Figs. 352-355). Edges of teeth serrated. Numerous small teeth on the palate. About twenty-seven presacral vertebrae. Neural spines simple, usually curved backwards in posterior lumbar and sacral region. Tail comparatively short. *D. gigas* Cope and

C. W., Mounted Skeleton of *Dimetrodon gigas*. Proc. U.S. Nat. Mus., vol. lvi., p. 525, 1919.—*Huene F. von*, *Ctenosaurus*. Centralbl. f. Min., etc., 1914, p. 496.—*Oxyodon*. *Loc. cit.*, 1908, p. 431.—*Matthew, W. D.*, A four-horned Pelycosaurian from the Permian of Texas. Bull. Amer. Mus. Nat. Hist., vol. xxiv., p. 183, 1908.—*Romer, A. S.*, The Permo-Carboniferous Reptile *Dimetrodon*. Journ. Geol., vol. xxxv., p. 673, 1927.—*Tilton, J. L.*, Permian Vertebrate Tracks in West Virginia. Bull. Geol. Soc. America, vol. xlii., p. 547, 1931.—*Williston, S. W.*, *Sphenacodon* Marsh. Proc. Nat. Acad. Sci. Washington, vol. ii., p. 650, 1916; also in Public. Carnegie Inst. Washington, no. 181, p. 61, 1913.

other species 1 m. to 3 m. long. Texas, New Mexico, and Oklahoma. Supposed footprints in the Waynesburg Sandstone of West Virginia.

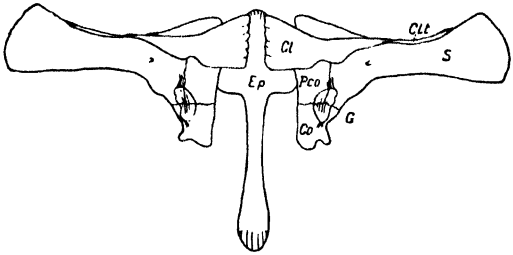


FIG. 354.
Dimetrodon dollovianus Case. Diagram of pectoral arch, ventral view. Permian; Texas. *Cl*, clavicle; *Clt*, cleithrum; *Co*, coracoid; *Ep*, interclavicle; *G*, glenoid fossa; *Pco*, precoracoid; *S*, scapula. Much reduced (after Case).

Bathygnathus Leidy. Permian; Prince Edward Island, Canada.

? *Tetraceratops* Matthew. Rugosities for paired horns on prefrontals and premaxillae. *T. insignis* Matthew, known only by skull about 10 cm. long. Baylor County, Texas.

Oxyodon F. von Huene. Maxilla only. Permian; Kenilworth, Warwick.

Ctenosaurus F. von Huene. Cervical and dorsal vertebrae with very long, laterally compressed, smooth neural spines. *C. koeneni* F. von Huene, with some spines 60 cm. long. Middle Bunter Sandstone;

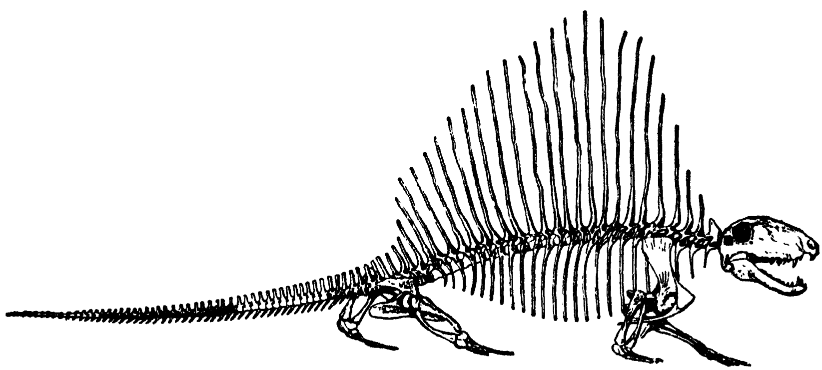


FIG. 355.
Dimetrodon. Skeleton restored. Permian; Texas. 1/23 nat. size (after Romer).

Göttingen. Same or nearly similar genus in Permian of New Mexico and Texas, U.S.A. (*C. rugosus* Case).

Family 7. **Edaphosauridae.**[1]

Skull short, low, and laterally compressed, tapering to snout, with tooth-bearing border of maxilla nearly straight, and teeth partly conical, partly laterally compressed. Neural spines very long, with transverse processes, forming a crest along the back. Two sacral vertebrae. Cleithrum present. Humerus with ectepicondylar as well as entepicondylar foramen. Lower Permian probably to Triassic.

[1] *Case, E. C.*, Mounted Skeleton of *Edaphosaurus cruciger*. Occas. Papers Mus. Zool. Univ. Michigan, no. 62, 1918; also in Public. Carnegie Inst. Washington, no. 181, p. 71, 1913.—*Fritsch, A.*, *Naosaurus mirabilis*. Sitzb. k. böhm. Ges. Wiss., math.-naturw. Cl., 1895, p. 2.—*Jaekel, O.*, *Naosaurus credneri*. Zeitschr. Deutsch. Geol. Ges., vol. lxii., Monatsb. p. 526, 1910.—*Osborn, H. F.*, Mounted Skeleton of *Naosaurus*. Bull. Amer. Mus. Nat. Hist., vol. xxiii., p. 265, 1907.

Edaphosaurus Cope. Large orbits far back and overhung by cranial roof; large lachrymal bone reaching external narial opening. Numerous small teeth on palate. Twenty-six presacral vertebrae. Abdominal ribs present. *E. pogonias* Cope and other species 2 m. to 3 m. long. Lower Permian; Texas, New Mexico, and Pennsylvania.

Naosaurus Cope (Fig. 356). As *Edaphosaurus*, but neural spines of neck distally expanded. Lower Permian; Texas. Vertebrae also in Lower Permian of Bohemia and the Ural, Russia, and in the Middle Permian near Dresden.

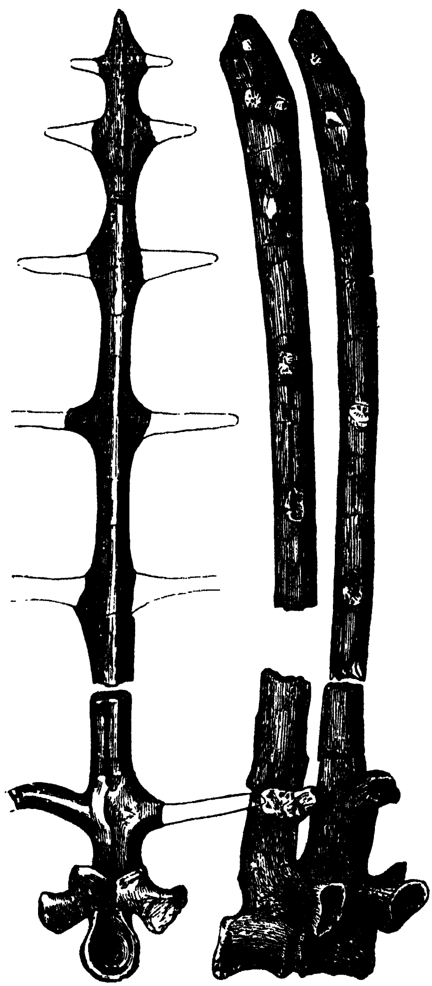


FIG. 356.
Naosaurus claviger Cope. Dorsal vertebrae, anterior and lateral aspects. Permian; Texas. 1/4 nat. size (after Cope).

Sub-Order 2. DINOCEPHALIA.[1]

Skull massive, with the large pineal foramen opening in a protuberance or boss; face relatively small, with a pair of external narial openings on top, not terminal. Occipital face flattened, overlapped by postparietal and tabular bones above, and pierced by a pair of small posterior temporal vacuities; occipital condyle single, with small pit for notochord; squamosal and quadrate very long and large; no secondary palate; coronoid process in mandible small or absent; teeth only in premaxillae, maxillae, and dentaries. Crown of each tooth raised into a stout cusp externally, but forming a more or less hollowed crushing surface internally. Vertebrae deeply amphicoelous, sometimes pierced by notochord; no intercentra behind axis; three or four sacral vertebrae. Limbs and their supporting arches massive; precoracoid scarcely entering glenoid fossa; scapula without acromion; a rudimentary cleithrum. [*Phalangeal formula unknown.*]

This Sub-Order includes heavy animals, often two to three metres in length, with the limbs a little sprawling. The Tapinocephaloids must have been herbivorous, but the Titanosuchids may have been carnivorous.

[1] *Broom, R.*, Further Comparison of South African Dinocephalians with the American Pelycosaurs. Bull. Amer. Mus. Nat. Hist., vol. xxxiii., p. 135, 1914.—*Nopcsa, F.*, Some Fossil Reptiles from the Copper-bearing Permian Strata of Russia. Geol. Hungarica, Ser. Palaeont., vol. i., p. 12, 1928.—*Watson, D. M. S.*, The Deinocephalia. Proc. Zool. Soc., 1914, p. 749.

Family 1. **Tapinocephalidae.**[1]

Face short and broad; canines not much enlarged. Permian.

Tapinocephalus Owen. Snout much depressed, broad and rounded, with a uniform row of teeth having large pulp cavities. Width of cranium behind greater than total length of skull. Postorbital and zygomatic arches very broad, so that the orbits and temporal vacuities are relatively small. *T. atherstonei* Owen, with skull about 45 cm. long. Karroo Formation (Lower Beaufort Beds); South Africa. The skull described as *Mormosaurus* Watson,

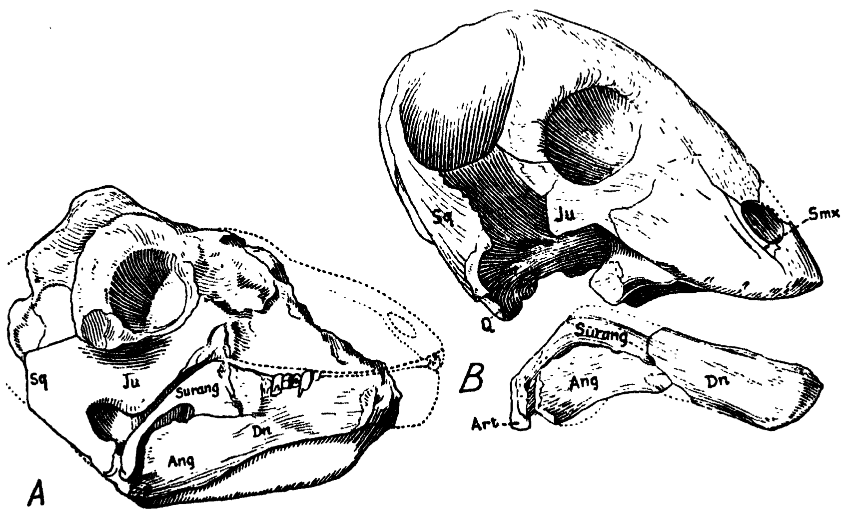


FIG. 357.

Skulls with mandible of (*A*) *Delphinognathus conocephalus* Seeley and (*B*) *Moschops capensis* Broom. Karroo Formation (Lower Beaufort Beds); South Africa. *Ang*, angular; *Art*, articular; *Dn*, dentary; *Ju*, jugal; *Q*, quadrate; *Smx*, septomaxilla; *Sq*, squamosal; *Surang*, surangular. $^1/_6$ nat. size (after W. K. Gregory and Broom).

and the vertebrae and limb bones named *Phocosaurus* Seeley, may belong to the same genus.

Pnigalion Watson; *Struthiocephalus* Haughton; *Taurops*, *Pelosuchus*, *Moschognathus* Broom. Lower Beaufort Beds; South Africa.

Eccasaurus Broom. Humerus and perhaps a tooth from Upper Ecca Beds, South Africa.

Moschops Broom (Fig. 357, *B*). Snout rising gradually to the brain-case, not depressed. *M. capensis* Broom, known by most of the skeleton, with skull about 40 cm. long. Lower Beaufort Beds; South Africa.

Delphinognathus Seeley (Fig. 357, *A*). Skull much resembling that of *Moschops*, but pineal eminence more prominent. *D. conocephalus* Seeley. Lower Beaufort Beds; South Africa.

Keratocephalus F. von Huene. Anterior part of frontal region raised into

[1] *Broom, R.*, *Moschops.* Proc. Zool. Soc., 1911, p. 1073.—*Taurops. Loc. cit.*, 1912, p. 859. —*Gregory, W. K.*, Skeleton of *Moschops capensis* Broom. Bull. Amer. Mus. Nat. Hist., vol. lvi., p. 179, 1926.—*Haughton, S. H.*, New Dinocephalian [*Struthiocephalus*] from the Gouph. Ann. S. African Mus., vol. xii., p. 52, 1915.—*Seeley, H. G.*, *Delphinognathus conocephalus* Seeley. Quart. Journ. Geol. Soc., vol. xlviii., p. 469, 1892.

a conical bony horn-core. *K. moloch* F. v. H., with skull 50 cm. long. Lower Beaufort Beds; South Africa.

Family 2. **Titanosuchidae.**[1]

Face comparatively large and elongated; canines enlarged. Permian.

Titanosuchus Owen. Jaws with four or five pairs of incisiform teeth, and ten or eleven pairs of teeth behind the enlarged canines. *T. ferox* Owen. Karroo Formation (Lower Beaufort Beds); Gouph, South Africa.

Jonkeria Van Hoepen (Fig. 358). Skull nearly twice as long as its maximum width; facial portion not deeper than wide; no supraorbital bony bosses. Nasal bones separated for about three-quarters of their length by a backward extension of the premaxillae. Five pairs of upper, four pairs of lower incisiform

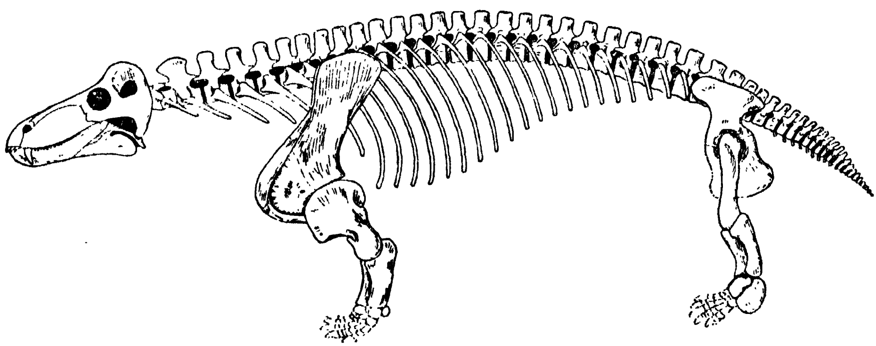


FIG. 358.

Jonkeria truculenta Van Hoepen. Restoration of skeleton. Karroo Formation (Lower Beaufort Beds); Prince Albert District, South Africa. About $^1/_{36}$ nat. size (after Broom). Compare with restoration of *Keratocephalus moloch* by F. von Huene, Geol. u. Palaeont. Abhandl., n.f., vol. xviii., pls. x., xi., 1931.

teeth; seventeen teeth in maxilla behind the canine. Atlas forming complete ring, with unusually large intercentrum. *J. truculenta* Van Hoepen, and other species, from Karroo Formation (Lower Beaufort Beds), Prince Albert District, South Africa. Type skull about 55 cm. long.

Anteosaurus Watson. Hinder portion of cranium very wide, with a pair of large supraorbital bony bosses; facial portion deep and narrow. *A. magnificus* Watson, with skull more than 50 cm. long. Lower Beaufort Beds; Tamboer Fontein, South Africa.

Dinocynodon, Dinophoneus, Dinosphageus, Enobius, Phoneosuchus, Scapanodon, Scullya Broom; *Lamiasaurus* Watson; ?*Dinartamus* Broom. With two pairs of large caniniform teeth in lower jaw. Lower Beaufort Beds; South Africa.

Mnemiosaurus Nopcsa. Permian; Ural, Russia.

Deuterosaurus Eichwald, as re-described by Nopcsa, may belong to a distinct family. Squamosal not in contact with the postorbital. *D. biarmicus* Eichw. Permian; Ural, Russia.

[1] *Broom, R.*, Carnivorous Mammal-like Reptiles of the Family *Titanosuchidae*. Ann. Transvaal Mus., vol. xiii., p. 9, 1929.

Family 3. **Moschosauridae.**[1]

Primitive Titanosuchids with long, low, narrow skull, and pineal eminence comparatively small. Permian.

Moschosaurus Haughton. Roof of brain-case not much thickened; post-orbital bar very narrow; nasals forming prominent ridge between the nostrils and orbits. *M. longiceps* Haughton, with skull about 25 cm. long. Lower Beaufort Beds; Beaufort West, South Africa.

Sub-Order 3. DROMASAURIA.

Small Theromorphs of slight build, with slender legs and long tail. Skull short, with very large orbits, the pair of large narial openings laterally placed, and the squamosal with a long downward process over the quadrate; coronoid process in mandible small or absent; teeth small and uniform or absent. Vertebrae amphicoelous and pierced by notochord; cervicals with intercentra; two or three sacral vertebrae. Abdominal ribs present. Scapula without acromion. Phalangeal formula, 2, 3, 3, 3, 3.

Family 1. **Galechiridae.**

Teeth present. No coronoid process in mandible. Permian.

Galechirus Broom.[2] Premaxillary teeth larger than maxillary teeth; orbit with sclerotic plates. At least sixty vertebrae in tail. Digits with large claws. *G. scholtzi* Broom, with humerus 35 mm. and femur 38·5 mm. long. Lower Beaufort Beds; Victoria West, South Africa.

Galepus Broom. Same formation near Richmond Road, Cape Colony.

? *Macroscelesaurus* Haughton.[3] Hind limbs relatively long. Same formation near Victoria West. May be a Therocephalian.

Family 2. **Galeopsidae.**

Toothless. A small coronoid process in mandible. Permian.

Galeops Broom.[4] Skull and lower jaw very short and deep. *G. whaitsi* Broom, with skull 4 to 5 cm. long. Lower Beaufort Beds; near Beaufort West, South Africa.

Sub-Order 4. DICYNODONTIA.

(*Anomodontia* auct.)

Skull large and massive with relatively small face, paired narial openings, a pineal foramen, and very large temporal fossae, from which the parietal bones are excluded by the union of the postorbital with the squamosal. Usually a median preparietal bone in front of pineal foramen; squamosal very large, triradiate, forming a

[1] *Haughton, S. H.*, New Type of Dinocephalian (*Moschosaurus longiceps*). Ann. S. African Mus., vol. xii., p. 78, 1915.
[2] *Broom, R.*, Trans. S. African Phil. Soc., vol. xviii., p. 31, 1907.
[3] *Haughton, S. H.*, Ann. S. African Mus., vol. xii., p. 175, 1918.
[4] *Broom, R.*, Proc. Zool. Soc., 1912, p. 860.

long pedicle for the relatively small quadrate and quadrato-jugal, which both enter the articular condyle; occipital face flattened, with postparietal and tabular bones above, without posterior temporal vacuities; occipital condyle tripartite, formed by basi-occipital and exoccipitals. Vomer single in domed roof of mouth, with descending plates of palatines and maxillae forming an incipient secondary palate; an inter-pterygoid vacuity; premaxillae fused and mandibular symphysis solid, forming a toothless beak, probably sheathed with horn during life; palate toothless; maxilla toothless or with a single pair of persistently growing tusks, sometimes also with one or more rows of small conical teeth within the sharp outer edge; dentary toothless, or with small teeth to oppose the row of maxillary teeth when present; no coronoid process in mandible. About seven cervical, eighteen to twenty-one dorso-lumbar, and four to six sacral vertebrae; a proatlas; no intercentra. Scapula with acromion; a rounded ossification (spongy bone) in sternum; a cleithrum present. Phalangeal formula, 2, 3, 3, 3, 3.

The Dicynodonts or Anomodonts vary much in size, some being only as large as rats, others somewhat larger than a tapir. Most of them are heavily built, with a relatively large head, and must have lived on land. A few (*Lystrosaurus*), with sharply turned-down face, and the eye and nostril high up, seem to have been aquatic. The nature of their food is unknown. Their remains are most abundant, and represent most numerous genera and species, in the Karroo Formation of South Africa, where they range from the Middle or Upper Permian to the Upper Triassic. They have also been found in corresponding formations in India, N. Russia, N. Scotland, Brazil, and perhaps in N. America.

The bones of the skull tend to fuse together, so that the sutures are often obscure. The most noteworthy element is the large triradiate squamosal; and the small quadrate at the lower end of its descending ramus sometimes appears to be only loosely articulated. Traces of a ring of sclerotic plates in the orbit are often observable.

Family 1. **Dicynodontidae.**[1]

Jaws toothless, or with only a single pair of maxillary tusks. Permian and Triassic.

Dicynodon Owen (*Oudenodon*, *Platypodosaurus* Owen; *Aulacocephalus*, *Dicranozygoma*, *Eurycarpus*, *Keirognathus*, *Rhachiocephalus*, *Rhachicephalodon* Seeley) (Figs. 359, 360). Parieto-frontal region of skull gradually passing

[1] *Broom, R.*, Structure and Affinities of *Udenodon*. Proc. Zool. Soc., 1901, p. 162.—Differences in the Skulls of Dicynodonts apparently due to Sex. *Loc. cit.*, 1902, p. 86.—Shoulder Girdle in *Lystrosaurus*. Ann. S. African Mus., vol. iv., p. 139, 1903.—Structure of the Dicynodont Skull. *Loc. cit.*, vol. vii., p. 337, 1912.—Internal Ear in *Dicynodon*. Proc. Zool. Soc., 1912, p. 419.—New Genera and Species of Anomodont Reptiles. *Loc. cit.*, 1921, p. 647.—*Haughton, S. H.*, Descriptive Catalogue of the Dicynodontia. Ann. S. African Mus., vol. xii., p. 127, 1915.—Skull of *Kannemeyeria*. *Loc. cit.*, vol. xii., p. 91, 1915.—*Hoepen, E. C. N. van*, *Lystrosaurus*. Ann. Transvaal Mus., vol. iv., pp. 1, 208, 1913–14; vol. v., pp. 70, 215, 1915–16.—*Huene, F. von*, *Dicynodon* Schädel. Palaeont. Zeitschr., vol. v., p. 58, 1922.—*Newton, E. T.*, New Reptiles from the Elgin Sandstones. Phil. Trans. Roy. Soc., vol. 184 B, p. 431, 1893.—*Pearson, H. S.*, Skull of *Kannemeyeria*. Proc. Zool. Soc., 1924, p. 793.—A Dicynodont Reptile Reconstructed. *Loc. cit.*, 1924, p. 827.—*Sollas, I. B. J.*, and *Sollas, W. J.*, Study of the Skull of a Dicynodon by means of Serial Sections. Phil. Trans. Roy. Soc., vol. 204 B, p. 201, 1913.—Structure of the Dicynodont Skull. *Loc. cit.*, vol. 207 B, p. 531, 1916.—*Watson, D. M. S.*, Skeleton of *Lystrosaurus*. Rec. Albany Mus., vol. ii., p. 287, 1912.—Limbs of *Lystrosaurus*. Geol. Mag. [5], vol. x., p. 256, 1913.

into the facial region; no parietal crest; maxillae with pair of tusks in male, toothless in female (named *Oudenodon* by Owen). Limb bones have been described as *Platypodosaurus* Owen (Fig. 361). *D. lacerticeps*, *leoniceps* Owen, and numerous other species with skull up to 60 cm. in length, from the Karroo Formation (Lower Beaufort Beds) of South Africa, including Nyasaland (about Middle Permian to Upper Triassic). Also from Upper Permian of N. Dwina, Russia.

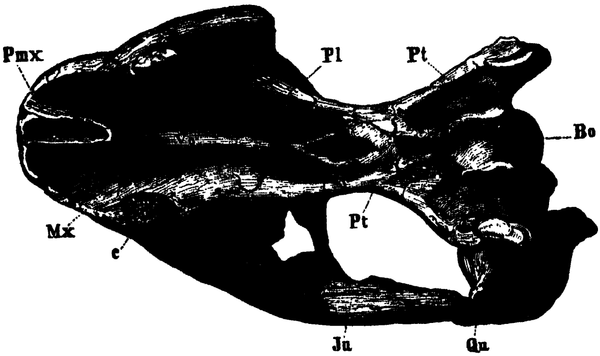


FIG. 359.

Dicynodon pardiceps Owen. Karroo Formation; Fort Beaufort, South Africa. Palatal aspect of skull. *Bo*, basioccipital; *c*, maxillary tusk (fractured); *Ju*, jugal; *Mx*, maxilla; *Pl*, palatine; *Pmx*, premaxilla; *Pt*, pterygoid; *Qu*, quadrate. $^1/_4$ nat. size (after Owen).

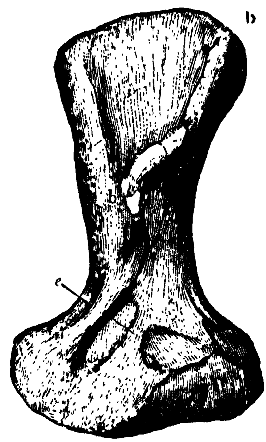


FIG. 360.

Dicynodon pardiceps Owen. Anterior aspect of humerus. *b*, delto-pectoral ridge; *e*, entepicondylar foramen. $^1/_4$ nat. size (after Owen).

Kannemeyeria Seeley. Skull as in *Dicynodon*, but with a narrow high parietal crest; pineal foramen in depression in front of crest. No tuskless skulls known. *K. simocephalus* Weithofer sp. and other species from the upper part of the Karroo Formation (Upper Beaufort Beds, *Cynognathus* Zone). A gigantic species of this or a

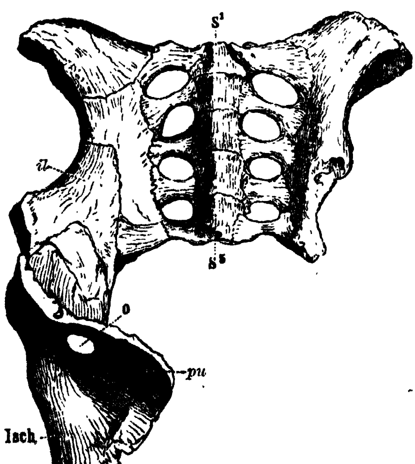


FIG. 361.

Platypodosaurus robustus Owen (= *Dicynodon*). Karroo Formation; South Africa. Ventral aspect of sacrum and right half of pelvis. *il*, ilium; *Isch*, ischium; o, obturator foramen; *pu*, pubis; *S*¹-*S*⁵, sacral vertebrae. $^1/_8$ nat. size (after Owen).

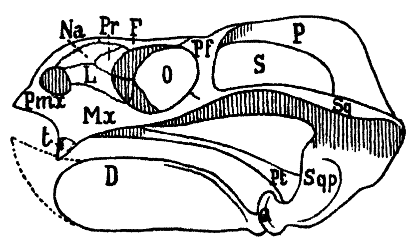


FIG. 362.

Gordonia traquairi Newton. Restoration of skull and mandible in left side view. Permian; Elgin, Scotland. *D*, dentary; *F*, frontal; *L*, lachrymal; *Mx*, maxilla; *Na*, nasal; *O*, orbit; *P*, parietal; *Pmx*, premaxilla; *Pf*, postfrontal; *Pr*, prefrontal; *Pt*, pterygoid; *Q*, quadrate; *S*, temporal vacuity and fossa; *Sq*, squamosal; *Sqp*, descending pedicle of squamosal; *t*, maxillary tusk. $^1/_3$ nat. size (after E. T. Newton and A. S. Woodward).

closely allied genus from the Triassic of Rio Grande do Sul, Brazil (F. von Huene).

Aulacocephalodon Seeley (*Bainia* Broom); *Diictodon*, *Eosimops*, *Eocyclops*, *Palemydops* Broom; *Chelyrhynchus* Haughton. Karroo Formation (Lower Beaufort Beds); South Africa. *Myosaurus* Haughton. Middle Beaufort Beds.

Gordonia Newton (Fig. 362). Skull as in *Dicynodon* but lighter and with very small tusks. Permian; Cuttie's Hillock, Elgin, Scotland.

Lystrosaurus Cope (*Ptychognathus* Owen *nec* Stimpson; *Ptychosiagum* Lydekker) (Figs. 363-366). Facial region of skull sharply bent downwards,

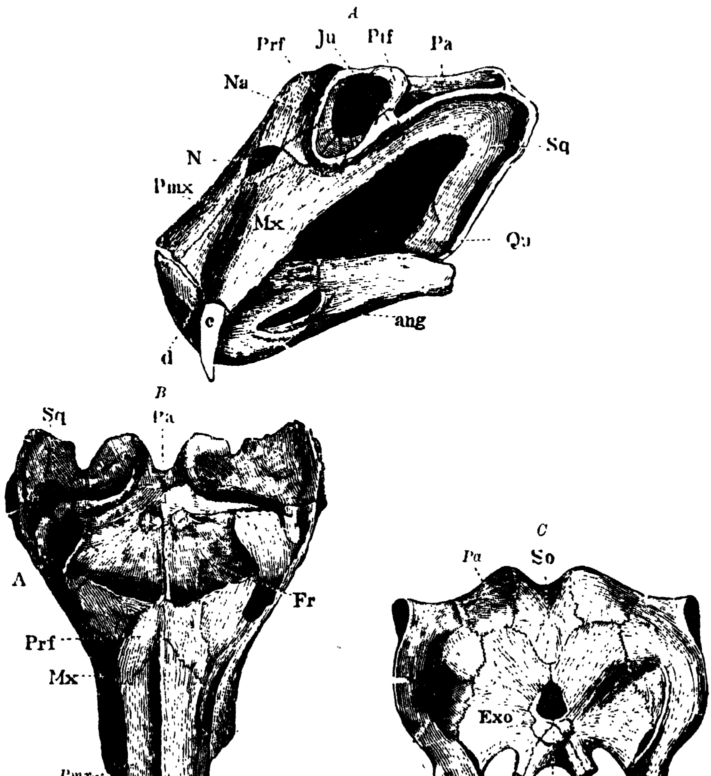


FIG. 363.

Lystrosaurus declivis Owen sp. Karroo Formation; Rhenosterberg, South Africa. Skull from lateral (*A*), superior (*B*), and posterior (*C*) aspects. *A*, orbit; *ang*, angular; *Bo*, basioccipital; *c*, maxillary tusk; *d*, dentary; *Exo*, exoccipital; *Fr*, frontal; *Ju*, jugal; *Mx*, maxilla; *N*, external narial opening; *Na*, nasal; *Pa*, parietal in figs. *A*, *B*, tabular in fig. *C*; *Pmx*, premaxilla; *Prf*, prefrontal; *Ptf*, postfrontal; *Qu*, quadrate; *So*, postparietal; *Sq*, squamosal. 1/3 nat. size (after Owen).

and narial openings near orbits. Maxillary tusks always present. Ring of sclerotic plates conspicuous. About twenty-five presacral vertebrae; the centra deeply amphicoelous. Limbs feeble. *L. declivis* Owen sp. and other species in the Karroo Formation (Middle Beaufort Beds) of South Africa. So-called *Dicynodon orientalis* Huxley, from the Lower Triassic (Panchet Group) of Bengal, India, and *Dicynodon incisivum* Repelin, from the Triassic of Indo-China, belong to this or a closely allied genus.

Geikia Newton. Skull like that of *Lystrosaurus*, but toothless. Permian; Cuttie's Hillock, Elgin, Scotland.

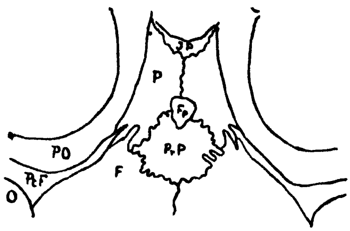


FIG. 364.

Lystrosaurus latirostris Owen sp. Diagram of middle part of cranial roof. Karroo Formation (Middle Beaufort Beds); South Africa. *F*, frontal; *Fp*, pineal foramen; *Jp*, postparietal; *O*, orbit: *P*, parietal; *PO*, postorbital; *PrP*, preparietal; *Ptf*, postfrontal. 1/2 nat. size (after Van Hoepen).

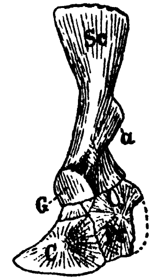


FIG. 365.

Pectoral arch of a Dicynodont (? *Lystrosaurus*). Karroo Formation; South Africa. *a*, acromion; *C*, coracoid; *G*, glenoid fossa for humerus; *Pc*, precoracoid; *Sc*, scapula. 1/4 nat. size (after Lydekker).

Prolystrosaurus Haughton. Intermediate between *Dicynodon* and *Lystrosaurus*. Middle Beaufort Beds; S. Africa.

Cistecephalus Owen. Perhaps representing a distinct family. Skull

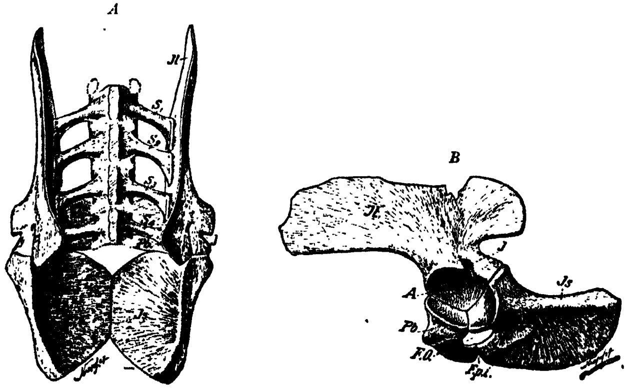


FIG. 366.

Lystrosaurus seeleyi Broili. Pelvis and sacrum from above (*A*) and from the left side (*B*). Karroo Formation; South Africa. *A*, acetabulum; *F.O*, obturator foramen; *Fpi*, ischio-pubic foramen; *J*, cleft in ilium; *Jl*, ilium; *Js*, ischium; *Pb*, pubis; S_1-S_4, sacral vertebrae. 1/3 nat. size (after Broili).

depressed, very broad, with wide parietal region, orbits much directed upwards; toothless. *C. microrhinus* Owen, with skull about 6 cm. long. Lower Beaufort Beds; S. Africa.

Family 2. Endothiodontidae.[1]

Maxilla and dentary with one or more rows of simple teeth; maxillary tusks apparently present only in males. Permian.

[1] *Broom, R.*, Structure and Affinities of the Endothiodont Reptiles. Trans. S. African Phil. Soc., vol. xv., p. 259, 1905.—*Diaelurodon*. Proc. Zool. Soc., 1911, p. 1075.—*Endothiodon*, etc. *Loc. cit.*, 1912, p. 866.

Endothiodon Owen (*Esoterodon* Seeley; *Endogomphodon* Broom). Teeth serrated in front and behind, in one principal row in each jaw, with smaller teeth sometimes within, sometimes without this row. Occipital condyle flattened or hollowed behind. Trunk about as broad as deep; twenty-eight presacral and four sacral vertebrae. *E. bathystoma* Owen, skull about 30 cm. long with deep parietal crest. *E. whaitsi* Broom, skull about 57 cm. long. Karroo Formation (Lower Beaufort Beds); South Africa, including Nyasaland.

Pristerodon Huxley (*Opisthoctenodon* Broom). Teeth serrated only on hinder edge, in one row. Successors seen on inner side. Lower Beaufort Beds; S. Africa.

Cryptocynodon, Tropidostoma Seeley; *Cerataelurus, Chelyoposaurus, Diaelurodon, Emydochampsa, Emydops, Emydopsis, Emydorhynchus, Emyduravus, Prodicynodon, Taognathus* Broom. Lower Beaufort Beds; S. Africa.

The following limb bones have been regarded as Dicynodont:

Brachybrachium Williston. Humerus from Trias, Wyoming, U.S.A.

Eubrachiosaurus Williston. Humerus, scapula, and pelvis from Trias, Wyoming, U.S.A.

Placerias Lucas. Humerus from Trias, Arizona, U.S.A.

Sub-Order 5. THERIODONTIA.

Carnivorous or insectivorous Theromorphs of light build, with the marginal teeth differentiated into incisors, canines, premolars, and molars, and the lower canines in front of the upper as in Mammals. Skull with face relatively large, terminal narial opening (single or paired), and usually a pineal foramen; a postparietal bone; squamosal very large; quadrate more or less reduced. Mandible with large coronoid process. Some intercentra between cervical vertebrae; two to four sacral vertebrae.

The Theriodonts vary in size from that of a weasel to that of a lion. Some of their skeletal remains from the Karroo Formation of South Africa can scarcely be distinguished from the corresponding parts of Mammals. According to Broom there are skulls (of *Ictidosauria*) with a secondary palate and paired occipital condyles, in which neither pineal foramen nor separate prefrontal, postfrontal, and postorbital bones can be distinguished. The diminutive quadrate is joined by the squamosal in forming an articulation for the mandible, in which the articular, angular, and surangular bones are mere rudiments. A median vomer separates the pterygoid bones in the palate. The incisor, canine, and premolar teeth in *Cyclogomphodon* are once replaced, the molars apparently without replacement. In a more primitive Cynodont (*Permocynodon*), however, Sushkin finds an irregular replacement of all the molariform teeth.

There are three well-defined groups or tribes of Theriodonts, the *Therocephalia, Gorgonopsia,* and *Cynodontia,* besides others which are still more imperfectly known.

Tribe 1. THEROCEPHALIA.[1]

Narrow intertemporal region of skull formed mainly by parietals, and pineal foramen large; no preparietal bone; occipital condyle single; no secondary palate;

[1] *Amalitzky, V. P., Anna petri* gen. et sp. nov. N. Dwina Researches, no. v., Acad. Sci. Leningrad, 1927 [in Russian].—*Broom, R., Ictidosuchus primaevus.* Trans. S. African Phil. Soc., vol. xi., p. 177, 1901.—New Primitive Theriodonts. Ann. S. African Mus., vol. iv., p. 147, 1903.—Skull

a pair of large suborbital vacuities in hinder part of palate. Symphysis of mandible slender and loose. Scapula without acromion; a rudimentary cleithrum. Phalangeal formula, 2, 3, 3, 3, 3.

Family 1. **Scaloposauridae.**

Skull shaped nearly like that of a dog, with more than three pairs of incisors in the upper jaw, and a uniform series of small simple teeth behind the canines. Permian.

Scaloposaurus Owen. Parietal region of skull nearly as wide as frontal region; postorbital bar incomplete; squamosal very slender. Upper teeth probably:—i. 6; c. 3; m. 9. *S. constrictus* Owen, known only by skull about 4 cm. long. Karroo Formation (Lower Beaufort Beds); Sneewberg, S. Africa.

Scylacosaurus Broom (Fig. 367). Dentary bone forming two-thirds the length of the mandible. Upper teeth:—i. 6; c. 2; m. 7; the outer incisor and anterior canine diminutive. Lower teeth:—i. 4; c. 1; m. 8; the outer incisor diminutive. A diastema behind the canines. Small teeth on pterygoids. *S. sclateri* Broom, known only by skull. Lower Beaufort Beds; Colesberg.

Pristerognathus Seeley. Only one canine and eight or nine molars in each jaw, six upper and three lower pairs of incisors. Base of Lower Beaufort Beds.

Hyaenasuchus, Trochosuchus, Lycosuchus Broom. With two large upper canines. Base of Lower Beaufort Beds.

Choerosaurus Haughton. Orbits in hinder half of skull, and postorbital bar apparently incomplete. A large bony boss on front part of each maxilla, and a smaller boss at lower border of hinder end of each dentary. Upper teeth:—i. 5; c. 3; m. 12; the two anterior canines relatively small. *C. dejageri* Haughton, with skull about 9 cm. long. Pelvis also known. Lower Beaufort Beds; Kuils Poort, Beaufort West.

Moschorhinus Broom. Snout unusually short and broad. Middle Beaufort Beds; New Bethesda Road. Allied to *Alopecopsis* Broom.

Alopecideops, Alopecodon, Alopecognathus, Alopecorhinus, Arnognathus, Cerdodon, Glanosuchus, Icticephalus, Ictidognathus, Ictidosuchus, Pardosuchus, Scylacoides, Scylacorhinus, Scymnosaurus, Simorhinella Broom; *Akidnognathus, Trochosaurus* Haughton; *Broomisaurus* Joleaud (*Scymnorhinus* Br.). Lower Beaufort Beds.

? *Theriodesmus* Seeley. A fore limb from the Karroo Formation of Klipfontein, Fraserberg, considered by Broom to be referable to a Therocephalian. The ulna bears a large olecranon process, and the phalangeal formula is 2, 3, 3, 3, 3.

Anna Amalitzky. Skull much resembling that of *Scylacosaurus*, but apparently with fewer teeth. *A. petri* Amal., with skull 23 cm. long. Permian; N. Dwina, Russia.

of new primitive Theriodont *Lycosuchus vanderrieti.* Trans. S. African Phil. Soc., vol. xiv., p. 197, 1903.—Two new Therocephalian Reptiles [*Glanosuchus*]. *Loc. cit.*, vol. xv., p. 85, 1904. —New Therocephalian Reptiles. Ann. S. African Mus., vol. iv., pp. 361, 369, 1908.—*Ictidognathus.* Proc. Zool. Soc., 1911, p. 1078.—*Pristerognathus, Alopecorhinus, Ictidognathus. Loc. cit.*, 1912, p. 863.—New Therocephalian Reptiles from the Karroo Beds of South Africa. *Loc. cit.*, 1920, p. 343.—*Haughton, S. H., Trochosaurus.* Ann. S. African Mus., vol. xii., p. 55, 1915.—New Carnivorous Therapsida. *Loc. cit.*, vol. xii., p. 180, 1918.—*Choerosaurus. Loc. cit.*, vol. xxviii., p. 60, 1929.—*Seeley, H* ..., *Theriodesmus phylarchus.* Phil. Trans. Roy. Soc., vol. 179 B, p. 141, 1888; *loc. cit.*, vol. 185 B, p. 1019, 1894.

The genus *Alopecopsis* Broom, known by a skull from the Lower Beaufort Beds, without any teeth behind the upper and lower canines, may represent

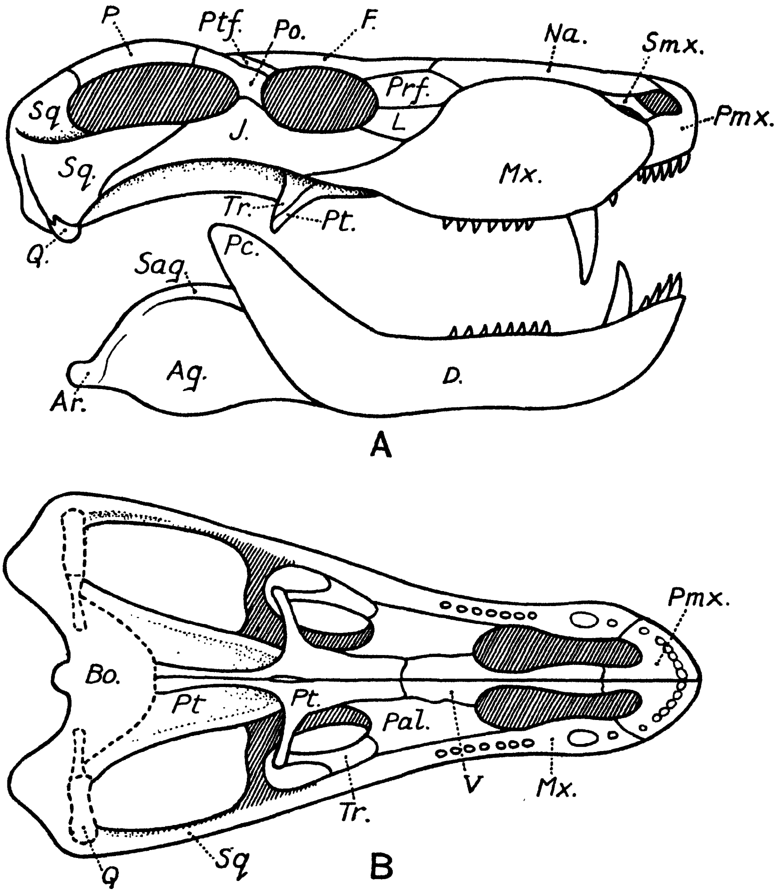


FIG. 367.

Scylacosaurus sclateri Broom. Skull and mandible in right side view (*A*) and palate (*B*). Karroo Formation (Lower Beaufort Beds); South Africa. *Ag*, angular; *Ar*, articular; *Bo*, basioccipital; *D*, dentary; *F*, frontal; *J*, jugal; *L*, lachrymal; *Mx*, maxilla; *Na*, nasal; *P*, parietal; *Pc*, coronoid process; *Pal*, palatine; *Pmx*, premaxilla; *Po*, postorbital; *Prf*, prefrontal; *Pt*, pterygoid; *Ptf*, postfrontal; *Q*, quadrate; *Sag*, surangular; *Smx*, septomaxilla; *Sq*, squamosal; *Tr*, transverse; *V*, vomer. $^1/_2$ nat. size (after Broom).

a distinct family. Allied to it are *Theriognathus* Owen, *Notosollasia* Broom, and *Whaitsia* Haughton, the latter known by numerous large skulls from the Lower Beaufort Beds, in which the suborbital vacuities are almost closed, and each antero-posteriorly elongated vacuity for the posterior nares is crossed by a bar of bone.

Tribe 2. GORGONOPSIA.

Intertemporal region of skull broad, the parietals being excluded from the temporal fossa by an upward and backward extension of the postorbital which reaches the squamosal; pineal foramen large; a preparietal bone; occipital condyle single; an

incipient secondary palate; no suborbital vacuities in palate. Symphysis of mandible massive. Scapula without acromion; sternum ossified. Phalangeal formula usually 2, 3, 4, 5, 3, rarely 2, 3, 3, 3, 3.

In most of the characters by which the *Gorgonopsia* differ from the *Therocephalia*, they agree with the *Dicynodontia*. The presence of a preparietal bone and an ossified sternum is especially noteworthy. The dentition shows that they were carnivorous.

Family 1. **Gorgonopsidae.**[1]

Skull long and narrow, with orbits smaller than temporal fossae. A uniform series of three to six (usually five) simple teeth behind the upper canine. Permian.

Gorgonops Owen. Skull depressed, with five pairs of upper incisors. *G. torvus* Owen, skull 20 cm. long. Karroo Formation (Lower Beaufort Beds); near Fort Beaufort, South Africa.

Scylacops Broom (Fig. 368). Septomaxillary large on face, edge of frontal excluded from orbit, and squamosal extending far forwards to meet the short jugal. A horizontal ridge along the maxilla and palatine on each side of the elongated internal narial openings, apparently for the attachment of a soft secondary palate. Few small teeth on palatines. *S. capensis* Broom. Lower Beaufort Beds; South Africa.

Lycaenops Broom. Upper teeth:—i. 5; c. 1; m. 4. Preparietal bone unusually large; small pineal foramen in the middle of a little raised boss. Probably twenty-seven presacral and three sacral vertebrae. *L. ornatus* Broom, with skull 25 cm. long, known by greater part of skeleton. Lower Beaufort Beds; Biesjespoort, South Africa.

Aelurosaurus Owen. Upper teeth:—i. 5; c. 1; m. 5. Clusters of small teeth on the pterygoid and palatine bones. Lower Beaufort Beds.

Arctognathus Broom. Upper teeth:—i. 4; c. 1; m. 5. *A. curvimola* Owen sp. Probably Lower Beaufort Beds; Kugaberg.

Aelurognathus Haughton. Upper teeth:—i. 5; c. 1; m. 4. Four of the five upper incisors unusually large. Phalangeal formula of fore foot, 2, 3, 4, 5, 3. Lower Beaufort Beds; probably also in Nyasaland.

Lycaenodontoides Haughton. Upper teeth:—i. 5; c. 1; m. 6. Top of skull pitted and rugose. In the type specimen of *L. bathyrhinus* H. the third and fourth digits of the fore foot contain only three phalanges, suggesting a phalangeal formula, 2, 3, 3, 3, 3. Lower Beaufort Beds; Oudeberg, Graaff Reinet.

Cynochampsa, Cynodraco, Lycosaurus, Tigrisuchus Owen; *Aloposaurus, Arctosuchus, Asthenognathus (Delphaciognathus), Cerdognathus, Cynarioides, Cynariops,*

[1] *Broom, R.*, The Gorgonopsia. Proc. Zool. Soc., 1913, p. 225; also *loc. cit.*, 1911, p. 1077 [*Aelurosaurus, Eriphostoma*], and 1912, p. 861 [*Scymnognathus*, etc.]; also Bull. Amer. Mus. Nat. Hist., vol. xxxii., p. 558, 1913 [*Scymnognathus*], and Ann. S. African Mus., vol. xii., p. 8, 1913 [*Scylacops*].—Structure of the Mammal-like Reptiles of the Sub-order Gorgonopsia. Phil. Trans. Roy. Soc., vol. 218 B, p. 345, 1930.—*Haughton, S. H.*, Some New Gorgonopsians [*Galesuchus, Gorgonognathus*]. Ann. S. African Mus., vol. xii., p. 82, 1915.—Some Gorgonopsian Skulls. *Loc. cit.*, vol. xii., p. 499, 1924; also *loc. cit.*, vol. xxviii., p. 68, 1929 [*Eoarctops, Lycaenodontoides, Hipposaurus*].—Karroo Vertebrates from Nyasaland [*Chiwetasaurus, Dixeya*]. Trans. Geol. Soc. S. Africa, vol. xxix., p. 69, 1926.—*Pravoslavlev, P. A.*, *Gorgonopsidae*. Acad. Sci. Leningrad, Amalitzky Exped., nos. iii., iv., *Inostransevia* and *Amalitzkia*, 1927 [in Russian].—*Watson, D. M. S.*, *Arctops, Scymnognathus*, etc. Proc. Zool. Soc., 1914, p. 1026.

Eriphostoma, Scylacognathus, Scymnognathus Broom; *Eoarctops, Galesuchus, Gorgonognathus, Hipposaurus, Scycosaurus* Haughton; *Arctops* Watson; *Lepto-*

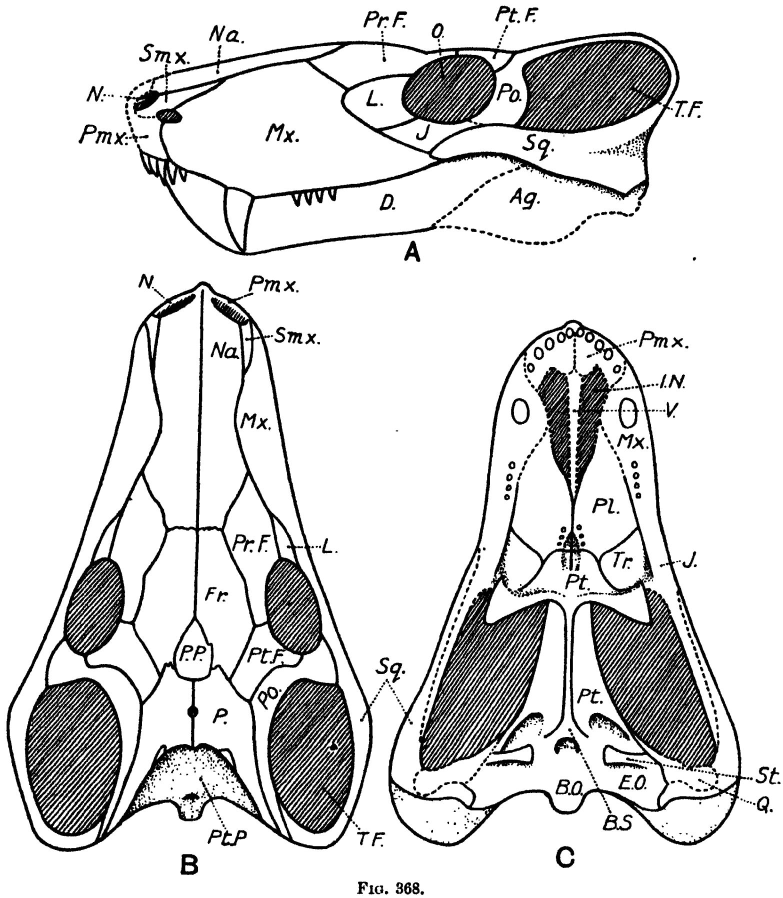


Fig. 368.

Scylacops capensis Broom. Skull and mandible in left side view (*A*), from above (*B*), and palate (*C*). Karroo Formation (Lower Beaufort Beds); South Africa. *BS*, basisphenoid; *EO*, exoccipital; *IN*, internal narial opening; *N*, external narial opening; *O*, orbit; *PP*, preparietal; *PtP*, postparietal; *St*, stapes; *TF*, temporal fossa; other letters as in Fig. 367. About $^1/_3$ nat. size (after Broom).

trachelus Watson (*nec* von der Marck). Lower Beaufort Beds; South Africa. *Chiwetasaurus, Dixeya* Haughton. Karroo Formation; Nyasaland.

Inostransevia Amalitzky. Upper teeth :—i. 4; c. 1; m. 4. Lower teeth :— i. 3; c. 1; m. 0. Upper incisors much larger than molars. *I. alexandri* Amal., with skull 50 cm. long, known by large part of skeleton. Permian; Northern Dwina, N.E. Russia.

Amalitzkia Pravoslavlev. Four large intercentra between the cervical vertebrae immediately behind the axis. Permian; Northern Dwina.

Rhopalodon Fischer; *Uraniscosaurus* Nopcsa.[1] Permian; Ural, Russia.

[1] *Nopcsa, F.*, Geologica Hungarica, Ser. Palaeont., vol. i., p. 13, 1928.

Family 2. **Ictidorhinidae.**[1]

Skull long and narrow with large frontal region, orbits larger than temporal fossae. Permian.

Ictidorhinus Broom. Upper teeth relatively small:—i. 4; c. 1; m. 5. Supraorbital region of skull raised, and pineal foramen opening in a small eminence. *I. martinsi* Broom, with skull 9·5 cm. long. Upper part of Lower Beaufort Beds; near New Bethesda.

Tribe 3. BAURIAMORPHA.[2]

Narrow intertemporal region of skull formed mainly by parietals, and pineal foramen small or absent; occipital condyle single; a secondary palate; a pair of large suborbital vacuities in hinder part of palate; an interpterygoid vacuity. Scapula without acromion; sternum rarely ossified. Phalangeal formula, 2, 3, 3, 3, 3.

Comprising a few genera which seem to be intermediate between the *Therocephalia* and the *Cynodontia*.

Bauria Broom. Occipital condyle divided by a deep groove. Postorbital bar incomplete. Upper teeth:—i. 4; c. 1; m. 10. The simple molars ground down smooth by wear. *B. cynops* Broom. Karroo Formation (Upper Beaufort Beds); South Africa.

Microgomphodon Seeley; *Aelurosuchus, Melinodon, Sesamodon* Broom. *Ericiolacerta* Watson. Upper and Middle Beaufort Beds; South Africa.

Tribe 4. CYNODONTIA.[3]

Narrow intertemporal region of skull formed mainly by parietals, and pineal foramen small or absent; prefrontal and postorbital usually meeting and excluding frontal from orbit; occipital condyle paired; no preparietal bone; a secondary palate into which the maxillae and palatines enter; no suborbital vacuities. Molar teeth more or less cusped. Scapula with acromion; sternum not ossified. Phalangeal formula, 2, 3, 4, 5, 3.

[1] *Broom, R.*, Bull. Amer. Mus. Nat. Hist., vol. xxxii., p. 560, 1913.

[2] *Watson, D. M. S.*, Some Carnivorous Therapsids. Proc. Zool. Soc., 1914, p. 1021.—Skeleton of a Bauriamorph Reptile. *Loc. cit.*, 1931, p. 1163.

[3] *Broom, R.*, Axis, Atlas, and Proatlas in the Higher Theriodonts. Proc. Zool. Soc., 1903, p. 177.—Skull in Cynodont Reptiles. *Loc. cit.*, 1911, p. 893.—*Ictidopsis. Loc. cit.*, 1912, p. 872.—*Lycognathus.* Bull. Amer. Mus. Nat. Hist., vol. xxxii., p. 557, 1913.—Mammal-like Dental Succession in Cynodont Reptiles. *Loc. cit.*, vol. xxxii., p. 465, 1913.—*Gomphognathus* and its Allies. Rec. Albany Mus., vol. iii., p. 227, 1919.—Some Recent new Light on the Origin of Mammals. Proc. Linn. Soc. N.S. Wales, vol. liv., p. 688, 1929.—*Gregory, W. K.*, and *Camp, C. L.*, Reconstruction of Skeleton of *Cynognathus.* Bull. Amer. Mus. Nat. Hist., vol. xxxviii., p. 538, 1918.—*Haughton, S. H.*, Some Upper Beaufort Therapsida. Trans. Roy. Soc. S. Africa, vol. x., p. 299, 1923.—*Huene, F. von*, Ein Cynodontier aus der Trias Brasiliens. Centralbl. f. Min., etc., 1928, Abt. B, p. 251.—*Petronievics, B.*, Comparison between the Lower Jaws of the Cynodont Reptiles *Gomphognathus* and *Cynognathus.* Proc. Zool. Soc., 1918, p. 197.—*Seeley, H. G.*, On *Diademodon.* Phil. Trans. Roy. Soc., vol. 185 B, p. 1029, 1894.—On the Gomphodontia. *Loc. cit.*, vol. 186 B, p. 1, 1895.—Skeleton in New Cynodontia *Loc. cit.*, vol. 186 B, p. 59, 1895.—*Sushkin, P. P.*, *Permocynodon*, a Cynodont Reptile from the Upper Permian of Russia. Internat. Congress Zool., Budapest, 1927, p. 804, 1929.—*Watson, D. M. S.*, Skull of *Diademodon.* Ann. Mag. Nat. Hist. [8], vol. viii., p. 293, 1911.

Family 1. **Cynognathidae.**

Molar teeth laterally compressed cones, with one or more pairs of basal denticles; lower molars biting within upper molars. Upper Permian and Triassic.

Cynognathus Seeley (Figs. 369, 370). Known by skull with definitely associated vertebral column and limb arches. Head remarkably large; and

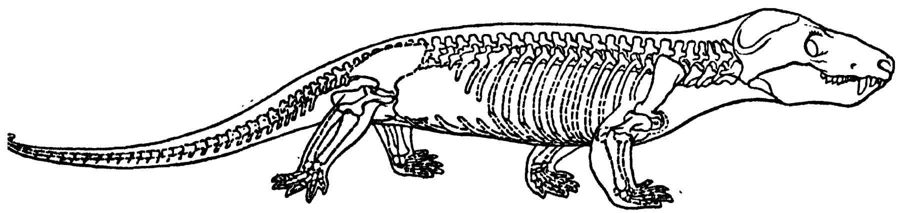


FIG. 369.

Cynognathus crateronotus Seeley. Restoration of skeleton. Karroo Formation (Upper Beaufort Beds); South Africa. About 1/20 nat. size (after Gregory and Camp).

back stiffened by the overlapping of expansions of the hinder dorsal and lumbar ribs. Skull with very broad postorbital bar and temporal arcade, and intertemporal crest elevated. Four pairs of serrated incisors in the upper jaw, probably three pairs in the mandible; canine partly serrated; five premolars and four molars in each jaw, also serrated and with a separate denticle at the base. Six or seven cervical vertebrae, seventeen or eighteen dorsals, four or five lumbars, and three or four sacrals. *C. crateronotus* Seeley (Fig. 369), with skull 40 cm. long and presacral vertebral column about 1 m. long; also *C. platyceps* Seeley (Fig. 370) and other species. Karroo Formation (Upper Beaufort Beds); South Africa.

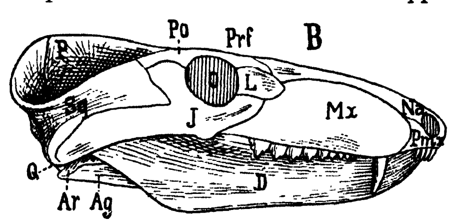


FIG. 370.

Cynognathus platyceps Seeley. Skull and mandible. Karroo Formation (Upper Beaufort Beds); South Africa. Lettering as in Fig. 367. About 1/4 nat. size (after Broom).

Cynidiognathus Haughton; *Lycochampsa* Broom (*Lycognathus* Broom). Upper Beaufort Beds.

The following imperfectly known genera may represent one or more distinct families:

Cynosuchus Owen; *Cynogomphius, Cynosuchoides* Broom. L. Beaufort Beds; S. Africa.

Galesaurus Owen. Skull depressed behind, compressed in front. Upper teeth:—i. 5; c. 1; m. 12. *G. planiceps* Owen, skull 10 cm. long. Middle Beaufort Beds; S. Africa.

Thrinaxodon Seeley. Angular and surangular bones larger than in *Cynognathus.* Upper teeth:—i. 4; c. 1; m. 7. Lower teeth:—i. 3; c. 1; m. 7. Variations in front teeth and premolars perhaps due to changes during dental succession. The phalangeal formula of both fore and hind foot is known to be 2, 3, 4, 5, 3. *T. liorhinus* Seeley. Upper Beaufort Beds; South Africa.

Tribolodon Seeley. Upper Beaufort Beds. *Glochinodon, Platycraniellus* van Hoepen. *Nythosaurus* Owen; *Ictidopsis* Broom. Middle Beaufort Beds.

Permocynodon Sushkin (Fig. 371). Cranial region of skull very long and broad, with high compressed intertemporal crest. A small pineal foramen. Angular and surangular bones as large as in *Thrinaxodon.* Upper teeth:—i. 5 or 6; c. 1; m. 12. Foremost three upper molars small and conical; next two larger and much swollen at base of crown; others larger, with one central cone, and two or three small additional cones on both the labial and lingual sides. According to Sushkin both the anterior and the posterior molariform teeth exhibit successional teeth. *P. sushkini* sp. nov., skull 9 cm. long, with maximum width of 6·5 cm. across zygoma. Upper Permian; N. Dwina, N. Russia. *Dwinia* Amalitzky, from the same formation and locality, is allied.

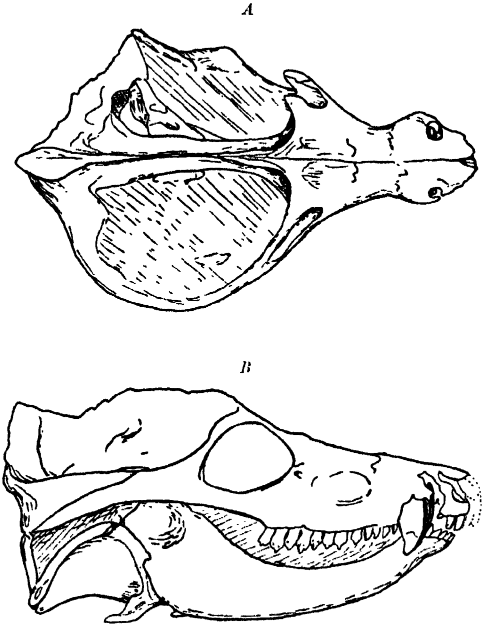


FIG. 371.

Permocynodon sushkini sp. nov. Skull and mandible, in top view (*A*) and right side view (*B*). Upper Permian; N. Dwina, N. Russia. 2/3 nat. size, drawn by Prof. P. P. Sushkin.

Family 2. **Diademodontidae.**

Molar teeth round in section or transversely extended, with cusped grinding surface; lower molars directly opposed to them. Triassic.

These Cynodonts were probably insectivorous or mixed feeders. They are grouped by Broom into genera as follows:

Diademodon Seeley. Narrow-headed form, with rounded upper molars and premolars. *D. tetragonus* Seeley, known only by fragment. Karroo Formation (Upper Beaufort Beds); Burghersdorp, South Africa.

Gomphognathus Seeley (Fig. 372). Broad-headed form; with most of the upper molars much broader than long. Upper teeth:—i. 4; c. 1; m. 9. *G. kannemeyeri* Seeley, *G. browni* Seeley sp., and other species. Upper Beaufort Beds; South Africa.

Cyclogomphodon, Octagomphus, Trirachodontoides Broom; *Protacmon* Watson. Upper Beaufort Beds.

Trirachodon Seeley. Skull not much widened behind. Upper incisors in three or four pairs, a stout canine, and from nine to eleven molars. Upper molars crowded and much laterally extended, the crown with three longitudinal ridges, of which the median is strongest and is most elevated at each end. *T. kannemeyeri* Seeley, skull 10 cm. long. Upper Beaufort Beds; Burghersdorp and Aliwal North, South Africa.

Gomphodontosuchus F. von Huene. Upper teeth:—i. 4; c. 1; m. 6. The first tooth of the molar series is minute and isolated. Other molars very irregular in shape, tending to be triangular, with margin beaded or crimped.

G. brasiliensis F. von Huene, skull about 18 cm. long. Triassic; near Santa Maria, Rio Grande do Sul, Brazil.

As already mentioned (p. 261), Broom regards the small rat-shaped *Ictidosauria* as another tribe of Theriodonts which are almost Mammals. They include the small jaws from the Stormberg Beds (Upper Triassic or Rhaetic) of South Africa named *Karoomys* and *Trithelodon* Broom, *Pachygenelus* Watson, and *Lycorhinus* Haughton.[1]

Another tribe, *Burnetiamorpha*, may be represented by the skull named *Burnetia* Broom, which is superficially like that of a Dinocephalian. It consists of spongy bone, with bosses above each orbit, one in each post-temporal region, and one on the nose. The pineal foramen is small. The incisors are reduced; there are four small molars and one canine. *B. mirabilis* Broom, skull about 19 cm. long. Karroo Formation (Middle Beaufort Beds); Water Krantz, South Africa. *Styracocephalus* Haughton, from the Lower Beaufort Beds, Beaufort West, South Africa, also known only by an imperfect skull, may be a related genus.[2]

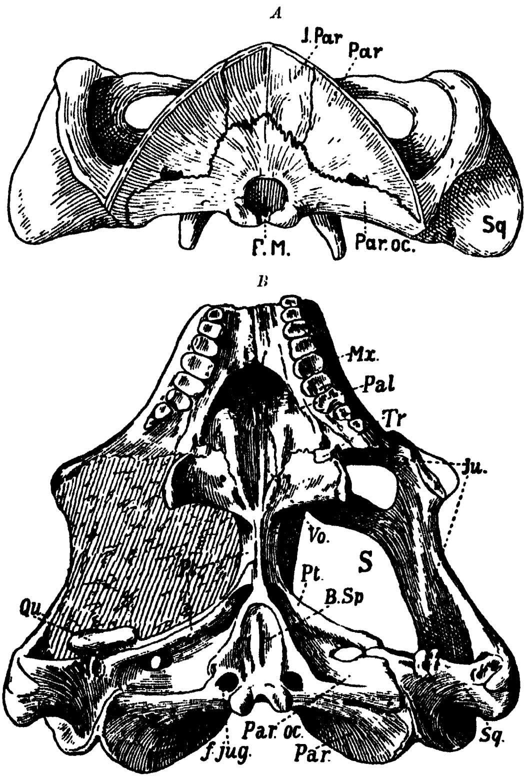


FIG. 372.

Gomphognathus browni Seeley sp. Skull lacking snout, in occipital view (*A*) and from below (*B*). Karroo Formation (Upper Beaufort Beds); South Africa. *B.Sp*, basisphenoid; *f.jug*, jugular foramen; *F.M.*, foramen magnum; *I.par*, postparietal; *Ju*, jugal; *Mx*, maxilla; *Pal*, palatine; *Par*, tabular; *Par.oc*, paroccipital (opisthotic); *Pt*, pterygoid; *Qu*, quadrate; *S*, temporal fossa; *Sq*, squamosal; *Tr*, transverse (ectopterygoid); *Vo*, vomer. $^4/_5$ nat. size (after Watson).

Order 3. ARAEOSCELIDIA.[3]

Primitive lizard-shaped land reptiles. Roofing bones of temporal region of skull contracting into a single broad arch; tabular and postparietal bones present; quadrate fixed. A pineal foramen. Conical teeth in sockets, some on the palate. Intercentra present; cervical ribs single-headed,

[1] *Broom, R.*, New type of Cynodont from the Stormberg. Ann. S. African Mus., vol. vii., p. 334, 1912.—*Karroomys*. Geol. Mag., p. 345, 1903.—*Haughton, S. H.*, *Trithelodon*, *Lycorhinus*. Ann. S. African Mus., vol. xii., p. 341, 1924.—*Watson, D. M. S.*, New Cynodont from the Stormberg. Geol. Mag. [5], vol. x., p. 145, 1913.

[2] *Haughton, S. H.*, Ann. S. African Mus., vol. xxviii., p. 55, 1929.

[3] *Broom, R.*, Skull of *Araeoscelis*. Proc. Zool. Soc., 1931, p. 741.—*Williston, S. W.*, Osteology of some American Permian Vertebrates. Journ. Geol., vol. xxii., p. 364, 1914.

dorsals partially double-headed, all articulating with the centra. No ossified pre-coracoid; pubis and ischium plate-like, the former pierced by a foramen; phalangeal formula, 2, 3, 4, 5, 4 (3).

Araeoscelis Williston (*Ophiodeirus* Broom) (Fig. 373). Marginal teeth in a nearly uniform series; palatal teeth minute. Very slender body and limbs; fore limb about as long as hind limb. At least seven cervical, twenty dorsal, and two sacral vertebrae, and a long slender tail. Coracoid and scapula fused together. Limb bones hollow; humerus with entepicondylar and ectepicondylar foramen. Abdominal ribs not observed. No armour. *A. gracilis* Will., about 80 cm. in length (Fig. 373). Permian; Texas.

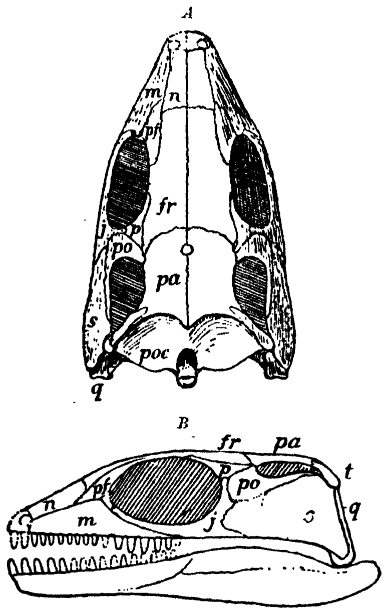


FIG. 373.
Araeoscelis gracilis Williston. Skull and mandible, in upper (*A*) and side view (*B*). Permian; Texas. Letters as in previous figs. Nat. size (after Williston).

The following imperfectly known genera of Permian reptiles may belong to this Order: *Protorosaurus* H. v. Meyer and *Gracilisaurus* Weigelt,[1] from German Kupferschiefer; *Adelosaurus* Watson, from English Marl Slate; *Parasaurus* Geinitz, from Zechstein of Thuringia; *Kadaliosaurus* Credner, from Niederhässlich, Dresden; *Aphelosaurus* Gervais from Autun, France.

The *Tanysitrachelia*, regarded by Peyer as a primitive Sub-Order of *Sauropterygia*, may also be related to the *Araeoscelidia.* They are slender lizard-shaped reptiles with a very long neck, known only by one genus:

Tanystropheus H. von Meyer (*Tribelesodon* Bassani; *Procerosaurus* F. v. Huene).[2] Head small; about twelve much elongated, hollow cervical vertebrae, which bear long and slender ribs, all single-headed except the last; fourteen dorsal vertebrae with ribs apparently single-headed; five sacral and pseudosacral vertebrae; and about forty-five caudals. Pelvis much like that of *Araeoscelis.* Three ossified elements in carpus, and three or four in tarsus; phalangeal formula, 2, 3, 4, 5, 3; terminal phalanges claws. Abdominal ribs numerous. No dermal armour. *T. longobardicus* Bassani sp., with the hinder teeth tricuspid in small individuals. Attaining a length of nearly a metre. Upper Triassic; Besano (Lombardy), Italy, and Serpiano (Tessin), Switzerland. *T. conspicuus* H. v. Mey., known by cervical (not caudal) vertebrae, sometimes nearly 30 cm. long, from the Upper Muschelkalk of Bavaria and Würtemberg. *T. antiquus* F. von Huene. Lower Muschelkalk; Upper Silesia.

[1] *Weigelt, J.*, Die vermutliche Nahrung von *Protorosaurus.* Leopoldina (Halle), vol. vi., p. 269, 1930.

[2] *Broili, F.*, *Tanystropheus conspicuus* H. v. Meyer. Neues Jahrb. f. Min., etc., 1915, vol. ii., p. 51.—*Edinger, T.*, Rückenmark in Wirbelkörper [*Tanystropheus*]. Anat. Anzeig., vol. lvii., p. 515, 1924.—*Huene, F. von*, *Tanystropheus* und verwandte Formen. Neues Jahrb. f. Min., etc., Beil.-Bd. 67, Abt. B, p. 65, 1931.—*Peyer, B.*, *Tanystropheus longobardicus* Bass. sp. Abhandl. Schweiz. Palaeont. Ges., vol. l., 1931.

Order 4. MESOSAURIA.[1] (*Proganosauria* Baur.)

Primitive amphibious or aquatic reptiles, with elongated head, short neck, elongated body, and very long tail. External nares separate, just in advance of the large orbits. Marginal teeth long and slender, in sockets; rows of smaller teeth on palate. Vertebral centra biconcave and pierced by notochord; no intercentra; two sacral vertebrae; ribs more or less thickened, single-headed, articulating with the centra. Abdominal ribs well developed. Coracoid with foramen; clavicular arch well developed; pubis and ischium plate-like; a pubic notch or foramen. Fore limb usually shorter than hind limb; humerus with entepicondylar foramen; four or five ossified distal carpal and tarsal bones; digital formula nearly 2, 3, 4, 5, 3, the fifth digit in hind foot lengthened.

As the hinder part of the skull in the *Mesosauria* has not yet been clearly observed, their systematic position is uncertain. Von Huene and Nopcsa assign them to the *Ichthyopterygia*; Seeley places them near the *Nothosauria*;

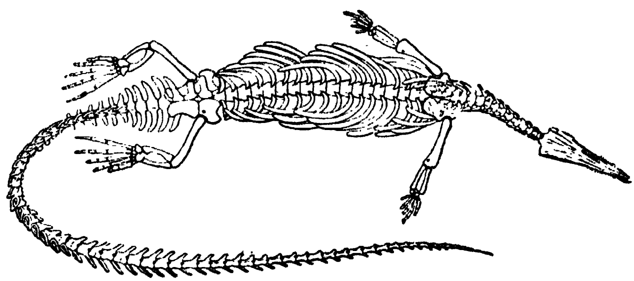


FIG. 374.
Stereosternum tumidum Cope. Ventral view of skeleton. Permian; San Paulo, Brazil. $^1/_5$ nat. size (after M'Gregor).

and M'Gregor regards them as primitive *Rhynchocephalia*. Wiman argues that they cannot be closely related to the *Ichthyopterygia*.

Mesosaurus Gervais (*Ditrochosaurus* Gürich). Skull longer than neck. Twenty-nine presacral vertebrae. Notch in pubis. Four phalanges in fifth toe of hind foot. *M. tenuidens* Gerv. Lower Karroo (Dwyka); South Africa. *M. brasiliensis* M'Gregor, usually nearly a metre in length. Permian; S. Paulo, etc., Brazil.

Stereosternum Cope (*Notosaurus* Marsh) (Fig. 374). Skull not longer than neck. Thirty-four presacral vertebrae. Foramen in pubis. *S. tumidum* Cope, about 80 cm. long. Permian; S. Paulo, Brazil.

Noteosaurus Broom. Six phalanges in fifth toe of hind foot. Lower Karroo; S. Africa.

[1] *Broom, R.*, Structure of *Mesosaurus*. Trans. S. African Phil. Soc., vol. xv., p. 103, 1904.—Species of *Mesosaurus*. Ann. S. African Mus., vol. iv., p. 379, 1908.—*Cope, E. D.*, Vertebrate Palaeontology of Brazil. Proc. Amer. Phil. Soc., vol. xxiii., p. 7, 1886.—*Geinitz, H. B.*, *Stereosternum tumidum* Cope. Ann. Soc. Géol. Belg., vol. xxv., p. 35, 1900.—*Gürich, G.*, *Ditrochosaurus capensis*. Zeitschr. Deutsch. Geol. Ges., vol. xli., p. 641, 1889.—*M'Gregor, J. H.*, *Mesosaurus brasiliensis* nov. sp. In *I. C. White*, Final Report, Commissão de Estudos das Minas de Carvão de Pedra do Brazil, p. 303. Rio de Janeiro, 1908.—*Seeley, H. G.*, Mesosauria of South Africa. Quart. Journ. Geol. Soc., vol. xlviii., p. 586, 1892.—*Stromer, E. von*, Fossilen Reptilreste aus Deutsch-Südwestafrika. Centralbl. f. Min., etc., 1914, p. 530 [bibliography].—*Wiman, C.*, Mesosaurier. In Festschrift f. Gorganovic-Kramberger. Zagreb, 1925.—*Woodward, A. S.*, New specimen of *Stereosternum*. Geol. Mag. [4], vol. iv., p. 145, 1897.

Order 5. ICHTHYOSAURIA.[1] (*Ichthyopterygia.*)

Primitive marine reptiles with fish-shaped body, long head and tail, and no distinct neck. Roofing bones of temporal region of skull contracting into a single broad arch ; quadrate fixed. Rostrum long and tapering ; orbits large, laterally placed, with sclerotic ring. External nares separate, slightly in advance of orbits. Pineal foramen and supratemporal vacuities large. Teeth usually conical and inserted in a continuous groove on the maxillae and elongated premaxillae and mandible, but sometimes wanting. Vomers toothless. Vertebrae numerous, very short, deeply amphicoelous. Ribs long, articulating only with centra ; abdominal ribs present. Pectoral arch consisting of coracoids, scapulae, clavicles, and a triangular or T*-shaped interclavicle ; sternum not ossified. Limbs short, paddle-shaped, sometimes with more than five rows of phalanges, and a layer of cartilage round the carpals, tarsals, and phalanges. No dermal armour. Viviparous.*

The members of this Order are distinguished chiefly by their fish-shaped body, paddle-shaped limbs with numerous oval or polygonal phalanges, large head with elongated rostrum, short amphicoelous vertebrae, and naked skin. In external form, limb-structure, and adaptation to a marine existence, they depart as widely from other reptiles as whales do from land mammals, and occupy as isolated a position. Like the whales, they doubtless evolved from land animals, for the fore paddles of the earlier (Triassic)

[1] *Andrews, C. W.*, Osteology of *Ophthalmosaurus icenicus*. Geol. Mag., 1907, p. 202.—Descriptive Catalogue of the Marine Reptiles of the Oxford Clay, pt. i. London, 1910.—Ichthyosaurian Paddle showing Traces of Soft Tissues. Proc. Zool. Soc., 1924, p. 533.—*Bauer, F.*, Die Ichthyosaurier des oberen weissen Jura. Palaeontogr., vol. xliv., p. 283, 1898.—*Ichthyosaurus bambergensis*. XVIII. Ber. Naturf. Ges. Bamberg, p. 1, 1900. — Osteologische Notizen über Ichthyosaurier. Anat. Anzeig., vol. xviii., p. 581, 1905.—*Baur, G.*, On the morphology and origin of the Ichthyopterygia. Amer. Nat., vol. xxi., p. 837, 1887 ; also Bericht 20. Versammlung Oberrhein. Geol. Vereins, p. 20, 1887 ; and Anat. Anzeig., vol. x., p. 456, 1894.—*Branca, W.*, Sind alle im Innern von Ichthyosauren liegenden Jungen ausnahmslos Embryonen ? Abh. K. Preuss. Akad. Wiss., 1907, p. 1, 1908 ; also Sitzb. K. Preuss. Akad. Wiss., phys.-math. Cl., vol. xviii., p. 392, 1908.—*Broili, F.*, Ein neuer Ichthyosaurus aus der norddeutschen Kreide. Palaeontogr., vol. liv., p. 139, 1907 ; see also *loc. cit.*, vol. lv., p. 295, 1909, and Neues Jahrb. f. Min., etc., Beil.-Bd. xxv., p. 422, 1908.—*Dollo, L.*, L'Audition chez les Ichthyosauriens. Bull. Soc. Belge Géol., etc., vol. xxi., Proc.-Verb., p. 157, 1907.—*Fraas, E.*, Die Ichthyosaurier der süddeutschen Trias und Jura Ablagerungen. Tübingen, 1891.—Die Hautbedeckung von Ichthyosaurus. Württ. Jahresh., 1894, p. 493.—Embryonaler Ichthyosaurus mit Hautbekleidung. *Loc. cit.*, 1911, p. 480. —Ein unverdrückter Ichthyosaurus-Schädel. *Loc. cit.*, 1913, p. 1.—*Gilmore, C. W.*, Osteology of *Baptanodon* (Marsh). Mem. Carnegie Mus., Pittsburgh, vol. ii., p. 77, 1905.—*Hawkins, T.*, Memoirs of Ichthyosauri and Plesiosauri. London, 1834.—*Huene, F. von*, Die Ichthyosaurier des Lias und ihre Zusammenhänge. Berlin, 1922.—Becken von *Ichthyosaurus quadriscissus*. Centralbl. f. Min., etc., 1922, p. 277.—Ichthyosaurier aus der Kreide Argentiniens. Rev. Mus. La Plata, vol. xxviii., p. 234, 1925 ; also Centralbl. f. Min., etc., 1925, p. 90.—Neue Ichthyosaurierfunde aus dem schwäbischen Lias. Neues Jahrb. f. Min., etc., Beil.-Bd. lv., Abt. B, p. 66, 1926.—*Myobradypterygius*. Centralbl. f. Min., etc., Abt. B, 1927, p. 22.—Ein neuer *Eurhinosaurus* aus dem oberen Lias von Holzmaden. Neues Jahrb. f. Min., etc., Beil.-Bd. lix., p. 471, 1928.—Neue Studien über Ichthyosaurier aus Holzmaden. Abhandl. Senckenb. Naturf. Ges. Frankfurt, vol. xlii., p. 345, 1931.—Neue Ichthyosaurier aus Württemberg. Neues Jahrb. f. Min., etc., Beil.-Bd. lxv., Abt. B, p. 305, 1931.—*Jaekel, O.*, Eine neue Darstellung von *Ichthyosaurus*. Zeitschr. Deutsch. Geol. Ges., vol. lvi., Protokoll, p. 26, 1904.—*Liepmann, W.*, Leichengeburt bei Ichthyosauriern. Sitzb. Heidelberg. Akad. Wiss., math.-nat. Kl., 1926, p. 8.—*Longman, H. A.*, Ichthyosaurian Skull from Queensland. Mem. Queensland Mus., vol. vii., p. 246, 1922.—*Owen, R.*, Monograph of the fossil Reptilia of the Liassic Formations, pt. iii. (Palaeontogr. Soc.), 1881.—Monograph of the fossil Reptilia of the Cretaceous Formations (*loc. cit.*), 1851.—*Seeley, H. G.*, On *Ophthalmosaurus*, etc. Quart. Journ. Geol. Soc., vol. xxx., p. 696, 1874.—On the skull of an Ichthyosaurus. *Loc. cit.*, vol. xxxvi., p. 635, 1880.—Reproduction of certain species of *Ichthyosaurus*. 50th Rep. Brit. Assoc., p. 68 (1880), 1881.—*Sollas, W. J.*, Skull of *Ichthyosaurus* studied in serial sections. Phil. Trans. Roy. Soc., vol. 208 B, p. 63, 1916.—*Stromer, E.*,

forms are less completely adapted for swimming than those of the later forms. They occur throughout the Mesozoic marine deposits, and are most abundant in the Lias, where complete skeletons are common, and most widely spread in the Cretaceous in nearly all parts of the world. In size they vary from 1 to 10 or 12 metres in length.

The absence of branchial arches and shape of the hyoid bones prove that the Ichthyosaurs breathed by lungs; and well-preserved skeletons in the Lias of England and Würtemberg, which contain several embryos in the abdominal cavity, show that they were viviparous. Coprolitic matter in some of the

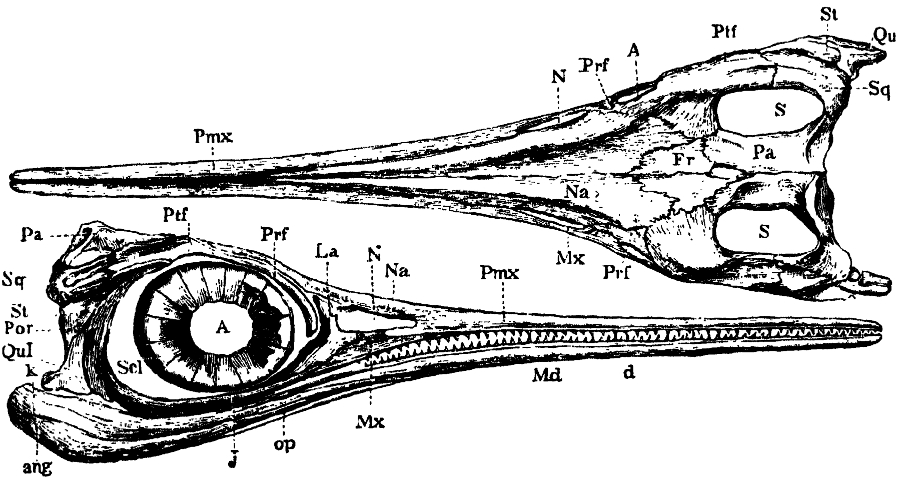


FIG. 375.

Stenopterygius zetlandicus Seeley sp. Skull, upper and lateral aspects. Upper Lias; Curcy, Calvados. *A*, orbit; *ang*, angular; *d*, dentary; *Fr*, frontal; *J*, jugal; *k*, surangular; *La*, lachrymal; *Md*, mandible; *Mx*, maxilla; *N*, external narial opening; *Na*, nasal; *op*, splenial; *Pa*, parietal; *Pmx*, premaxilla; *Por*, postorbital; *Prf*, prefrontal; *Ptf*, postfrontal; *QuJ*, quadrato-jugal; *S*, temporal vacuity; *Scl*, sclerotic plates; *Sq*, supratemporal or prosquamosal; *St*, squamosal. 1/4 nat. size (after E. Deslongchamps).

skeletons indicates that these reptiles fed chiefly on cuttle-fishes and fishes. It never bears any marks of the intestine, and the isolated coprolites with a spiral marking commonly ascribed to Ichthyosaurs probably belong to Hybodont sharks.

The *skull* (Fig. 375) is remarkable for its elongated, dolphin-like rostrum and enormous orbits, which are surrounded by a ring of fifteen to twenty sclerotic plates. The paired parietals and frontals are of small size, and a large pineal foramen occurs at their junction in the median line. Adjoining the parietals on either side are the large oval supratemporal vacuities (*S*), bounded externally by the supratemporal (or prosquamosal) and postfrontal. The external nares are triangular and placed close to the orbits; the nasals are extended in front, and the premaxillae greatly produced. The superior border of the orbit is formed by the postfrontal and prefrontal, the latter a

Neue Forschungen über Fossile Lungenatmende Meeresbewohner. Fortschr. naturwiss. Forschung, Berlin, vol. ii., p. 83, 1910.—*Theodori, C.*, Beschreibung des kolossalen *Ichthyosaurus trigonodon* zu Banz. Munich, 1854.—*Wiman, C.*, Beckengürtel bei *Stenopterygius quadriscissus*. Bull. Geol. Inst. Upsala, vol. xviii., p. 19, 1921. — *Woodward, A. S.*, Two specimens of *Ichthyosaurus* showing contained Embryos. Geol. Mag., 1906, p. 443.—The so-called Coprolites of Ichthyosaurians and Labyrinthodonts. *Loc. cit.*, 1917, p. 540.

narrow, triangular plate. In front of the orbit, and separating it from the narial opening, is a triangular lachrymal. A long, slender, rod-like jugal bounds the orbit below, and a curved oblique postorbital encloses it behind. Joining the postorbital and jugal posteriorly is the quadrato-jugal, which forms the postero-lateral angle of the skull, and with the quadrate enters the articulation for the lower jaw. An irregularly triangular or rectangular plate, the squamosal, is inserted between the quadrato-jugal and supra-temporal, and behind the postorbital and postfrontal. The maxilla is an elongate triangular bone, between the jugal, lachrymal, and premaxilla.

The basioccipital (Fig. 376) is very strongly developed, and bears a stout articular condyle. Above it and on either side of the foramen magnum are

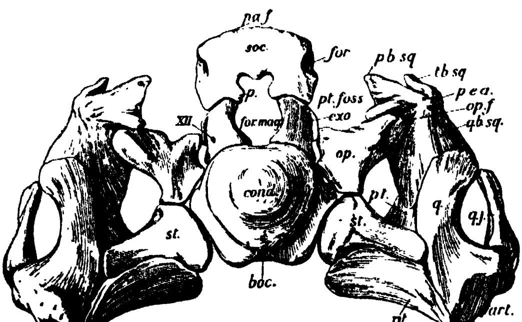


FIG. 376.

Ophthalmosaurus icenicus Seeley. Occipital view of skull. Oxford Clay; Peterborough. *art*, articular surface of quadrate; *boc*, basioccipital; *cond*, occipital condyle; *exo*, exoccipital; *for*, foramen in supraoccipital; *for.mag*, foramen magnum; *op*, opisthotic; *op.f*, facet for opisthotic; *p*, process of supraoccipital projecting into foramen magnum; *pa.f*, facet for parietal; *p.b.sq*, parietal branch of squamosal; *p.e.a*, postero-external angle of squamosal; *pt*, pterygoid; *pt.foss*, post-temporal fossa; *q*, quadrate; *q.b.sq*, quadrate branch of squamosal; *q.j*, quadrato-jugal; *soc*, supraoccipital; *st*, stapes; *t.b.sq*, temporal branch of squamosal; *XII*, foramen for posterior branch of hypoglossal nerve. $^1/_4$ nat. size (after C. W. Andrews).

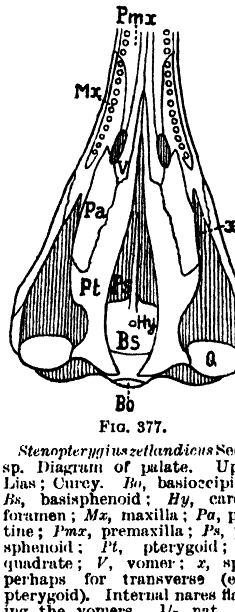


FIG. 377.

Stenopterygius zetlandicus Seeley sp. Diagram of palate. Upper Lias; Curcy. *Bo*, basioccipital; *Bs*, basisphenoid; *Hy*, carotid foramen; *Mx*, maxilla; *Pa*, palatine; *Pmx*, premaxilla; *Ps*, presphenoid; *Pt*, pterygoid; *Q*, quadrate; *V*, vomer; *x*, space perhaps for transverse (ectopterygoid). Internal nares flanking the vomers. $^1/_5$ nat. size (after A. S. Woodward).

the paired exoccipitals, capped by the supraoccipital. Outside the basioccipital and exoccipital of each side extends the rod-shaped stapes (or columella auris), which is relatively large and thick, and lies in a groove on the upper face of the pterygoid; its distal end fits into a shallow pit on the quadrate. Above this, adjoining the exoccipital, is the opisthotic, which remains separate from the proötic. The bones of the occipital and otic regions are rather loosely united, and the lateral walls of the brain case appear to have been cartilaginous; there is no ossified alisphenoid or orbitosphenoid. According to Dollo, hearing must have depended on the vibration of the bones of the skull, as in the *Cetacea*.

Abutting against the basioccipital on the lower side of the skull (Fig. 377) is the basisphenoid, which develops a long, splint-like anterior process (presphenoid), extending along the middle of a large interpterygoid vacuity. The basisphenoid is pierced by a single or double foramen for the carotid

arteries. The pterygoids are long and relatively large-sized bones joining the vomers and palatines in front, and the basisphenoid and quadrate behind. There is a well-developed columella or epipterygoid, but no transverse or ectopterygoid has been satisfactorily observed. The internal nares occupy their primitive position on either side of the narrow vomers A pair of stout, rib-like hyoid bones is present.

The slender rami of the lower jaw unite in an extensive symphysis, and are without a coronoid process. Each ramus consists of five or sometimes six pieces. A deep groove extends along the outer side of the dentary on its upper border, but becomes interrupted anteriorly into a series of pits for the blood-vessels.

The *teeth* (Fig. 378) in the post-Triassic genera are acutely conical, smooth or vertically striate, sometimes with anterior and posterior carinae, and even

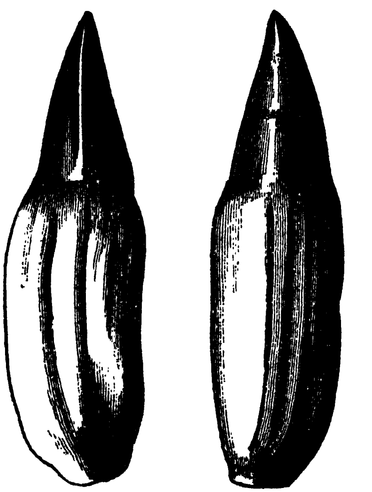


Fig. 378.
Leptopterygius platyodon Conyb. sp. Lower Lias; Lyme Regis. Tooth, lateral and anterior aspects. Nat. size (after Lydekker).

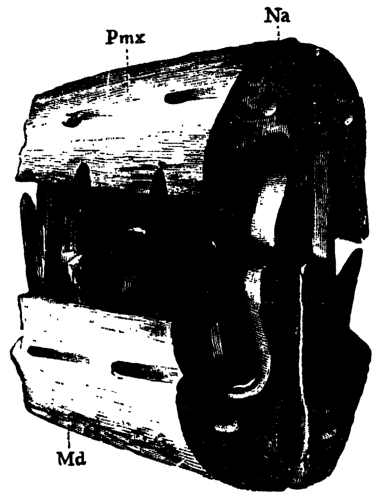


Fig. 379.
"*Ichthyosaurus*" *quenstedti* Zittel. Upper Jurassic; Würtemberg. Jaw-fragment, showing teeth in groove. *Md*, dentary; *Na*, nasal; *Pmx*, premaxilla. $^3/_4$ nat. size (after Quenstedt).

an incomplete third carina, and with a tumid root usually larger than the crown. As many as 180-200 occur in single series in upper and lower jaws (Fig. 379), being confined to the maxilla, premaxilla, and dentary. In the primitive Triassic forms the teeth are in sockets, but in the typical Ichthyosaurians they are placed in a deep groove, usually continuous, and were held in place by the soft tissues and the edges of the groove. Some of the later Mesozoic forms are toothless. The crown is composed of dentine, covered with a layer of enamel, and over this there may be sometimes still another layer of cement. A vertical folding of the walls of the root similar to that occurring in Labyrinthodonts is generally observed. The large root is composed of cement containing bone cells and vascular canals, enveloping a more or less folded cylinder of dentine.

The *vertebral column* comprises but two regions—caudal and precaudal. There is no true neck, and no sacrum. There are between 120 and 150

vertebrae, of which about 100 are caudal. The centra are extremely short, and deeply biconcave, as among Selachians and Labyrinthodonts. The neural arches are strongly developed, never fused with their centra, and articulate with one another by feeble zygapophyses. Adult individuals of the post-Triassic species almost invariably have the atlas and axis fused, and before and behind each of them are subvertebral hypocentra or intercentra. The remaining precaudal vertebrae are of nearly uniform character (Fig. 380), each centrum being provided with two pairs of tubercles for attachment with the double-headed ribs, and exhibiting dorsally a neural canal, with a rugose pit on either side for the pedicles of the neural arch. The anterior caudals bear only a single pair of tubercles for the support of the single-headed ribs, and these gradually disappear posteriorly (Fig. 381). The halves of the chevron bones usually remain separate, but the neural arch of each vertebra except the atlas is undivided. A downward deflection of the column occurs in the posterior part of the tail, where the vertebrae enter the base of the

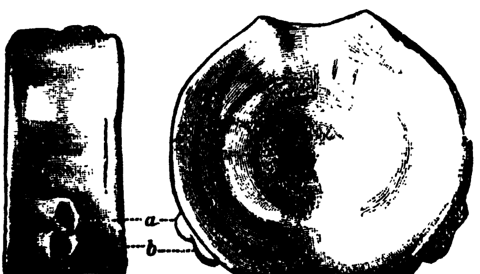


FIG. 380.
Macropterygius trigonus Owen sp. Posterior dorsal vertebra. Kimmeridge Clay; Wootton-Bassett, England. *a*, *b*, tubercular and capitular facets for ribs. 1/3 nat. size (after Lydekker).

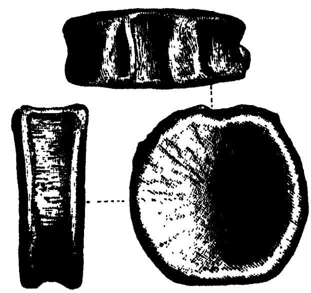


FIG. 381.
Ichthyosaurus sp. Caudal vertebra, from above, in side view, and in front view. Upper Lias; Banz, Franconia. Nat. size.

large, triangular caudal fin. The latter is expanded in a vertical plane, and between the Middle Triassic and Upper Jurassic periods it develops into a very powerful swimming organ. A median dorsal fin has also been observed (Fig. 386).

Ribs are present on all the precaudal vertebrae, and are longest between the tenth and thirteenth centra, after which they gradually decrease in size toward the pelvis. From hereon they continue single-headed, straight, and more like lateral processes than ribs, and disappear toward the caudal fin. The long slender ribs of the trunk are curved, subcylindrical in section, and in most species longitudinally grooved. A median and one or two paired lateral series of splint-like abdominal ribs are developed.

The *pectoral arch* (Fig. 382) is unusually powerful. There is no ossified sternum for the attachment of ribs, but a triangular or T-shaped interclavicle is present in the median line, in part overlapping the robust coracoids, whose inner edges meet in a long symphysis. The anterior border of each coracoid is somewhat deeply excavated, the posterior margin entire and rounded. Its lateral margin is developed into a short, stout, and thickened process bearing two articular facets, the foremost for receiving the proximal end of the scapula, and the hinder for the head of the humerus. The clavicles are

slender curved bones, usually meeting in the middle line at the anterior margin of the interclavicle. Their union may be either by suture or by fusion, or sometimes even by a joint.

Humerus, radius, and ulna are all short stout bones (Figs. 383, 384), and relatively much reduced. The proximal end of the humerus is thickened, the distal flattened and provided with radial and ulnar articular facets, which are remarkable for being concave. The remaining bones of the paddle, of which the first two rows correspond to the carpus, and the third to the metacarpus, are small and polygonal, and usually arranged in a mosaic. There are commonly from three to five digits, but as some of the phalangeal rows subdivide, the number of the latter is occasionally increased to eight or nine. As many as 100 phalanges are sometimes present. A deep incision is

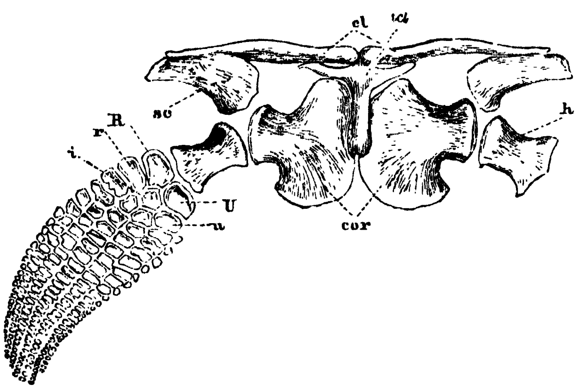


FIG. 382.

Ichthyosaurus communis Conyb. Pectoral arch and right fore limb, ventral aspect. Lower Lias; England. *cl*, clavicle; *cor*, coracoid; *h*, humerus; *i*, intermedium; *icl*, interclavicle (partly covered by clavicles); *R*, radius; *r*, radiale; *sc*, scapula; *U*, ulna; *u*, ulnare. 1/4 nat. size.

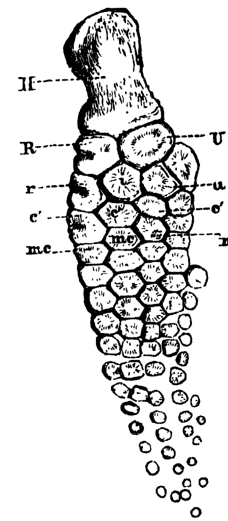


FIG. 383.

Stenopterygius triscissus Quenst. sp. Left fore paddle, dorsal aspect. Upper Lias; Boll, Wurtemberg. *c'*, distal carpals; *mc*, equivalents of metacarpals. Other letters as in Fig. 382.

often observable on the radius and three succeeding bones of the paddle (Fig. 383), the significance of which is not understood.

In the *pelvic arch* of the Triassic forms (Fig. 385, *A*), the pubis and ischium are expanded plates of considerable size, and the pubis is usually pierced by an obturator foramen. In the later typical Ichthyosaurians (Fig. 385, *B*), these two bones are reduced to slender rods with a distal expansion, and in some of the Middle and Upper Jurassic genera (*Ophthalmosaurus*) they are fused together. The ilium, which meets the other two elements in the acetabulum, is a comparatively slender bone, usually more or less arched and freely suspended in the muscles. The femur is short and stout, but relatively longer than the humerus; the rest of the hind paddle resembles the fore paddle.

Impressions of the smooth skin are shown in some specimens (Fig. 386), which display a soft dorsal and caudal fin, and a fringe of soft parts behind and below the bones of the paired paddles. A round sac of uncertain nature in the soft parts below the throat has also been observed by Abel. There is no dermal armour.

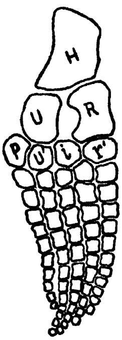


FIG. 384.

Mixosaurus cornalianus Bassani sp. Right fore paddle, dorsal aspect. Upper Triassic; Besano, Lombardy. *p*, pisiform; other letters as in Fig. 382.

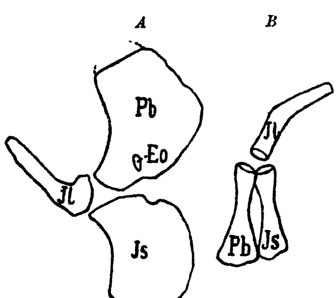


FIG. 385.

A, Right pelvic arch of *Cymbospondylus petrinus* Leidy, ventral aspect. Middle Triassic; Nevada. 1/7 nat. size (after Merriam). *B*, Left pelvic arch of *Ichthyosaurus communis* Conyb., outer aspect. Lower Lias; England. 1/5 nat. size (after A. S. Woodward). *Eo*, obturator foramen; *Jl*, ilium; *Js*, ischium; *Pb*, pubis.

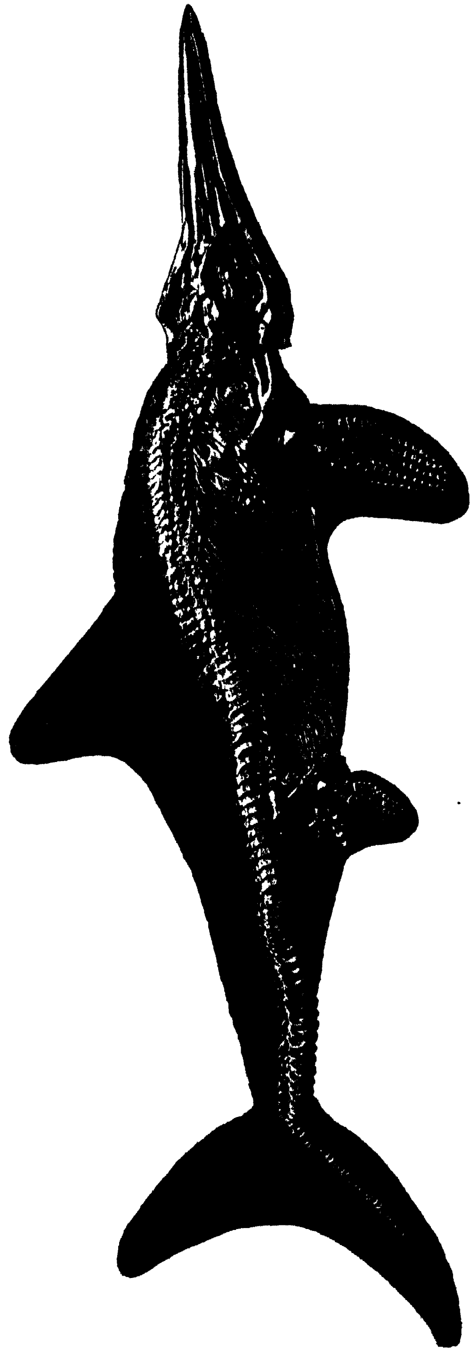


FIG. 386.

Stenopterygius quadriscissus Quenstedt sp. Skeleton about 2 metres long surrounded by remains of the soft parts, prepared by Dr. Bernhard Hauff. Upper Lias; Holzmaden, Würtemberg.

Family 1. **Omphalosauridae.**[1]

Maxilla and mandible with more than one row of blunt teeth in sockets. Triassic.

Omphalosaurus Merriam. Grinding teeth with a hemispherical crown and the root not vertically fluted; fixed in distinct sockets in three or more rows on the convex oral surface of the bone. *O. nevadanus* Merriam. Middle Triassic; Nevada, U.S.A.

Pessopteryx Wiman. Hemispherical grinding teeth with the root vertically fluted. *P. nisseri* Wiman. Middle Triassic; Spitzbergen. Isolated fragments.

Jaws from the Lower Muschelkalk of Jena ascribed to *Tholodus schmidti* H. von Meyer by K. von Fritsch (Abh. naturf. Ges. Halle, vol. xxiv., pl. viii., 1906) seem to belong to an Ichthyosaurian of this family.

Family 2. **Mixosauridae.**[2]

Teeth in a single row in sockets, mostly conical, low and blunt behind. Atlas and axis not fused. Ribs double-headed only in front part of trunk. Tail not much bent downwards. Interclavicle triangular. Humerus, radius, and ulna rather elongated, and the two latter not pressed together. Two digits articulating with intermedium of carpus. Pubis and ischium expanded. Triassic.

Mixosaurus Baur (Fig. 384). Anterior teeth relatively small and conical, posterior teeth laterally compressed and truncated. Root of teeth vertically fluted. Tail very long and gently bent downwards. Pelvic limbs much smaller than the pectoral limbs. *M. cornalianus* Bassani sp., from Upper Triassic of Besano, Lombardy, is known by nearly complete skeletons not more than 1 metre in length. *M. nordenskiöldi* Hulke sp., known by fragments from Middle Triassic of Spitzbergen. Species perhaps also in the Middle Triassic of Nevada, U.S.A., and Germany. This or an allied genus in the north of Dutch Timor, East Indies.

Phalarodon Merriam. Middle Triassic; Nevada.

? *Grippia* Wiman. Middle Triassic; Spitzbergen.

Family 3. **Shastasauridae.**[3]

As Mixosauridae, *but only one digit articulating with intermedium of carpus, and humerus, radius, and ulna sometimes short.* Triassic.

[1] *Merriam, J. C.*, New Marine Reptile from the Middle Triassic of Nevada. Bull. Dept. Geol. Univ. California, vol. v., p. 71, 1906.—*Merriam, J. C.*, and *Bryant, H. C.*, Dentition of *Omphalosaurus*. *Loc. cit.*, vol. vi., p. 329, 1911.

[2] *Broili, F.*, Über die Mixosauridae. Anat. Anzeig., vol. xlix., p. 474, 1916.—Mixosauridae von Timor. Wetensch. Meded. Dienst van den Mijnbouw in Nederl.-Indië, no. 17, 1931.—*Huene, F. von*, Beobachtungen an *Mixosaurus cornalianus* (Bassani). Centralbl. f. Min., etc., 1925, Abt. B, p. 289.—*Merriam, J. C.*, Skull and Dentition of a Primitive Ichthyosaurian [*Phalarodon*] from the Middle Triassic. Bull. Dept. Geol. Univ. California, vol. v., p. 381, 1910.—*Repossi, E.*, Il Mixosauro degli strati triasici di Besano in Lombardia. Atti Soc. Ital. Sci. Nat., vol. xli., p. 361, 1902.—*Wiman, C.*, Über *Mixosaurus cornalianus* Bass. sp. Bull. Geol. Inst. Upsala, vol. xi., p. 230, 1912.—Beckengürtel der Triasichthyosaurier. Palaeont. Zeitschr., vol. v., p. 272, 1922.—Eine neue marine Reptilien-Ordnung aus der Trias Spitzbergens. Bull. Geol. Inst. Upsala, vol. xxii., p. 183, 1928.

[3] *Dames, W.*, Ichthyopterygier der Triasformation. Sitzungsb. K. Preuss. Akad. Wiss., phys.-math. Cl., vol. xlvi., p. 1, 1895.—*Huene, F. von*, Shastasaurusreste in der alpinen Trias. Centralbl. f. Min., etc., 1925, Abt. B., p. 412.—Ichthyosaurier im deutschen Muschelkalk. Palaeontogr., vol. lxii., p. 1, 1916.—*Merriam, J. C.*, Triassic Ichthyosauria. Mem. Univ. California

Shastasaurus Merriam. Vertebral centra very short. Humerus, radius, and ulna much shortened, but usually a cleft between radius and ulna. *S. pacificus* Merriam. Upper Triassic (Upper Hosselkus Limestone); Shasta Co., California. The various species increase in size as they are traced upwards, ranging from about 3 to 10 metres in length.

Cymbospondylus Leidy (Fig. 385, *A*). Humerus, radius, and ulna relatively long and the two latter bones constricted in middle. Fore limb not much larger than hind limb. Facial region of skull relatively shorter than in *Ichthyosaurus*; basioccipital condyle concave. *C. petrinus* Leidy, probably about 10 metres in length. Middle Triassic; Nevada, U.S.A.

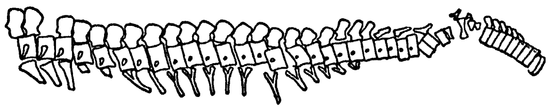


FIG. 387.

Delphinosaurus perrini Merriam. Vertebrae of tail showing downward bend at the extremity. Upper Triassic; California. 1/10 nat. size (after Merriam).

Merriamia Boulenger (*Leptocheirus* Merriam *nec* Germar). Caudal vertebrae elongated. Fore limbs much larger than hind limbs. Three digits and rudiments of a fourth, with laterally notched phalanges. *M. zitteli* Merriam. Upper Triassic; Shasta Co., California.

Toretocnemus, *Delphinosaurus* Merriam (Fig. 387). Vertebral centra longer than usual. Upper Triassic; Shasta Co., California.

Pessosaurus Wiman. Intermedium separating lower ends of radius and ulna. Middle Triassic; Spitzbergen.

? *Ekbainacanthus* Yakowlew. Triassic; Spitzbergen.

Vertebrae and other fragments from the Muschelkalk of Germany, Austria, and Roumania have also been provisionally referred to some of the above genera and to *Pachygonosaurus* F. von Huene. Undetermined genera occur in the Triassic of the Peace River, British Columbia, and of Timor, East Indies.

Family 4. **Ichthyosauridae**.

Teeth conical, with strong vertical flutings on the root, in a single row in a continuous groove. Atlas and axis fused. Ribs of trunk double-headed, of tail single-headed. Vertical tail fin supported by end of backbone sharply bent downwards. Interclavicle T*-shaped. Bones of limbs shortened and closely pressed together. Intermedium of carpus separating distal ends of radius and ulna and bearing two digits. Pubis and ischium narrow, sometimes fused and only separated by a small foramen.* Jurassic and Cretaceous.

These Ichthyosaurs form the Latipinnate Group of Kiprijanoff and Lydekker, and are grouped with the *Mixosauridae* in the family *Latipinnatidae* by von Huene and Nopcsa.

Ichthyosaurus König (*Proteosaurus* Home; *Gryphus* Wagler; *Eurypterygius* Jaekel) (Figs. 381, 382, 385, *B*). Jaws of equal length, and teeth extending in regular series along the whole length of the mouth. Humerus with two

vol. i., no. 1, 1908.—*Simionescu, I.*, Ichthyosaurierreste aus der Trias von Dobrogea. Bull. Acad. Roumaine, Sect. sci., ann. 1, p. 81, 1913.—*Wiman, C.*, Marine Triassic Reptile Fauna of Spitzbergen. Bull. Dept. Geol. Univ. California, vol. x., p. 63, 1916.—*Yakowlew, N.*, Neue Funde von Trias-Sauriern auf Spitzbergen. Verh. K. Russ. Min. Ges., vol. xl., p. 179, 1902, and vol. xli., p. 165, 1904.

distal facets (rarely with a small facet for intermedium between); not less than five digits in the fore limb, all completely ossified and closely pressed together for most of their length. Pubis and ischium not fused. A single soft dorsal fin. *I. communis* and *I. intermedius* Conybeare are represented by fine skeletons in the Lower Lias of Dorset (Lyme Regis), Somerset, and other parts of England; the former attaining a length of over 5 metres, the latter of over 2 metres. *I. breviceps* Owen and *I. conybeari* Lydekker, also from English Lower Lias. Incompletely known species also in the Lower Oolites of England and Würtemberg, and Lower Jurassic of East Greenland.

Ophthalmosaurus Seeley (*Sauranodon* Marsh *nec* Jourdan; *Baptanodon* Marsh; *Microdontosaurus* Gilmore) (Fig. 376). Jaws of equal length, teeth few and small, rudimentary, or absent. Orbit relatively large. Humerus with three distal facets for radius, ulna, and pisiform; not less than five digits in the fore limb, and all the phalanges cartilaginous round their margin. Pubis and ischium fused. *O. icenicus* Seeley, known by nearly complete skeletons from Oxford Clay of Peterborough. *O. natans* Marsh sp. Upper Jurassic; Wyoming, perhaps also South Dakota, U.S.A., and E. Greenland.

Apatodonsaurus Mehl. Jurassic; Wyoming.

Brachypterygius F. von Huene. Very broad fore paddle, the intermedium articulating with the humerus between the radius and ulna. *B. extremus* Boulenger sp.[1] Kimmeridge Clay; Dorset.

Macropterygius F. von Huene (Fig. 380). Upper Jurassic.

Myopterygius F. von Huene. Root of teeth with very thick layer of cement. Humerus with very strong deltoid ridge. *M. campylodon* J. Carter sp. Cenomanian (Lower Chalk); England. Other species in the Upper Cretaceous of France, Germany, Italy, Russia, India, Ceram, Australia, New Zealand, North and South America.

Myobradypterygius F. von Huene. Lower Cretaceous; Santa Cruz, Patagonia.

Family 5. Stenopterygiidae.

As Ichthyosauridae, *but only one digit articulated with intermedium of carpus.* Rhaetic, Jurassic, and Lower Cretaceous.

These Ichthyosaurs form the Longipinnate Group of Kiprijanoff and Lydekker, and are grouped with the *Shastasauridae* in the family *Longipinnatidae* by von Huene and Nopcsa.

Stenopterygius Jaekel (Figs. 375, 377, 383, 386). Jaws of equal length, and teeth extending in regular series along the whole length of the mouth. Heads of each presacral rib well separated. Fore paddle with four digits, usually broad. Pubis and ischium fused. *S. quadriscissus* Quenstedt sp. (Fig. 386). Upper Lias; Würtemberg. *S. zetlandicus* Seeley sp. (Figs. 375, 377), the largest species 4 to 5 m. long. Upper Lias; Whitby. Species perhaps also in the Lower Oolites.

Leptopterygius F. von Huene (*Temnodontosaurus* Lydekker) (Fig. 378). Jaws of equal length, and dentition complete. Heads of each presacral rib united by a flange of bone. Fore paddle with four digits, usually narrow and long. Pubis and ischium separate. The largest and stoutest species of

[1] *Boulenger, G. A.*, Proc. Zool. Soc., 1904, p. 424. The discoverer of this fossil informed A. S. Woodward that he obtained it from the Kimmeridge Clay near Weymouth.

the Lias, sometimes probably over 10 m. in length. *L. tenuirostris* and *L. platyodon* Conybeare sp., *L. latifrons* König sp., *L. lonchiodon* Owen sp. Lower Lias; England. *L. acutirostris* Owen sp. (*Ichthyosaurus trigonodon* Theodori). Upper Lias; Whitby, Bavaria, Würtemberg, and Dept. Yonne, France. Species perhaps also in the Rhaetic of France, Germany, and England (*I. rheticus* Sauvage). To the last species probably belong a neural arch and ischium named *Rachitrema pellati* Sauvage.

Eurhinosaurus Abel. As *Leptopterygius*, but upper jaw much longer than the lower jaw and the teeth comparatively small and feeble, though extending the whole length of both jaws. *E. longirostris* Jaeger sp., about 5 m. long. Upper Lias; Bavaria and Würtemberg, perhaps also Whitby.

Nannopterygius F. von Huene. Heads of each presacral rib well separated. Paddles very small. *N. entheciodon* Hulke sp. Kimmeridge Clay; Dorset and Boulonnais.

Platypterygius F. von Huene. Aptian; Hanover.

Cetarthrosaurus Seeley. Cambridge Greensand.

Order 6. PLACODONTIA.[1]

Primitive amphibious or aquatic reptiles, with short neck, small tail, and elongated paired limbs. Roofing bones of temporal region of skull forming a single broad arch; quadrate fixed; pterygoids and palatines meeting in middle line; vomer single. External nares separate, just in advance of orbits; a large pineal foramen. Crushing teeth on palatines, maxillae, and dentaries. Vertebrae amphicoelous; cervical ribs double-headed, articulating with centrum and neural arch; dorsal ribs single-headed, articulating with neural arch; a plastron of abdominal ribs. Scapulae well separated by a stout clavicular arch. The three pelvic bones entering the acetabulum; pubis and ischium plate-like. Bony dermal armour extensive.

Placodonts are known only from the marine Trias and Lias of Europe. They are remarkable for their peculiarly modified dentition, which is unparalleled among reptiles. The pavement-like crushing teeth, which were originally ascribed to fishes, attain considerable size, and exhibit flat or slightly arched crowns, usually dark-coloured in the fossils, and smooth or finely wrinkled. They are replaced by successional teeth developed beneath them.

Placodus Agassiz (*Anomosaurus* F. v. Huene) (Figs. 388, 389). Skull longer than broad, superiorly arched, the snout somewhat produced. Premaxillae and symphysis of lower jaw with cylindro-conical incisors. On each palatine and dentary there are three nearly rectangular pavement teeth; the maxilla has a single series of depressed, bean-shaped teeth. According to

[1] *Broili, F.*, Osteologie des Schädels von *Placodus*. Palaeontographica, vol. lix., p. 147, 1912. —Ein neuer Placodontier aus dem Rhaet der bayerischen Alpen. Sitzb. Bay. Akad. Wiss., math.-phys. Cl., 1920, p. 311.—*Drevermann, F.*, Über *Placodus*. Centralbl. f. Min., etc., 1915, p. 402. —Das Skelett der Placodontier. Palaeont. Zeitschr., vol. iv., p. 98, 1922.—Schädel und Unterkiefer von *Cyamodus*. Abhandl. Senckenberg. Naturf. Ges., vol. xxxviii., p. 291, 1924.—*Edinger, T.*, Zentralnervensystem von *Placodus gigas* Ag. Abhandl. Senckenberg. Naturf. Ges., vol. xxxviii., p. 311, 1925.—*Huene, F. von*, Reptilien der Trias. Geol. u. Palaeont. Abhandl., n.f., vol. vi., p. 1, 1902.—Ergänzungen zur Kenntnis des Schädels von *Placochelys* und seiner Bedeutung. Geol. Hungarica, Ser. Palaeont., fasc. 9, 1931.—*Jaekel, O.*, *Placochelys placodonta*. Result. wiss. Erforsch. Balatonsees, vol. i., p. 1, 1907.—*Meyer, H. von*, Unterkiefer von *Placodus andriani*. Palaeontogr., vol. x., p. 59, 1862; also vol. xi., 1863.—*Owen, R.*, Description of the skull and teeth of *Placodus laticeps*. Phil. Trans. Roy. Soc., vol. xlix., p. 169, 1858.—*Peyer, B.*, *Placodontia*. Abh. Schweiz. Palaeont. Ges., vol. li., p. 1, 1932.

Drevermann, the vertebrae are deeply amphicoelous, eight in the neck, twenty in the trunk, six in the sacrum, and thirty to forty in the tail. The neural arches bear a zygosphene-zygantrum articulation. The dermal armour consists of small isolated bones. The greater part of a skeleton in the Senckenberg Museum, Frankfurt, was found in the Upper Muschelkalk near Heidelberg. *P. gigas* Ag. has skull about 22 cm. in length. Detached teeth are abundant

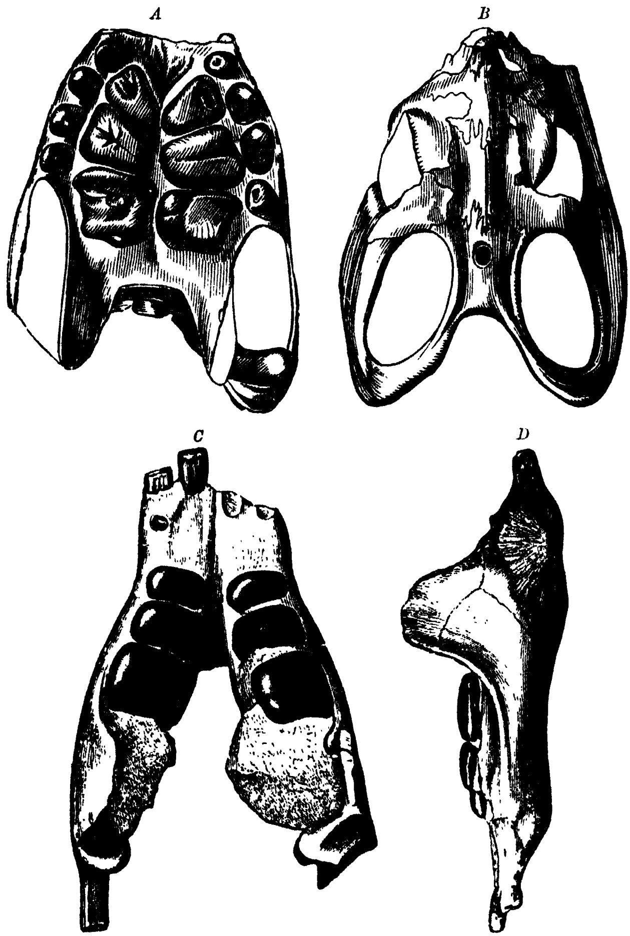


FIG. 388.

Placodus gigas Ag. Muschelkalk; Bayreuth, Germany. *A*, Palatal, and *B*, upper aspects of skull; *C*, oral, and *D*, lateral aspects of mandible. 1/3 nat. size.

in the Muschelkalk of Southern Germany and France, rare in the Wellendolomite and Alpine Keuper; one in Lias of Tessin, Switzerland.

Cyamodus H. v. Meyer. Skull triangular, snout much compressed. Each palatine bears a row of two or three rounded or elliptical crushing teeth, the hindmost at least twice the size of the anterior. The maxillary and premaxillary teeth are relatively small and few. Each dentary bears a large

tooth behind, two or three small teeth in front. *C. rostratus* Münster sp., skull 15 cm. long. Muschelkalk; Bavaria. Also Tessin, Switzerland.

Placochelys Jaekel (Fig. 390). Skull triangular, with very small laterally

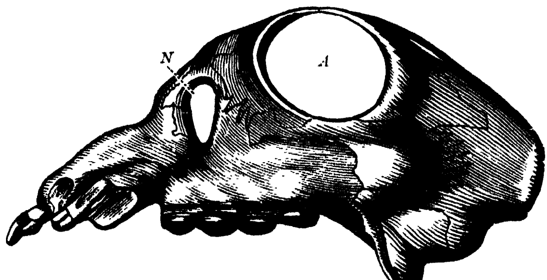


Fig. 389.
Placodus hypsiceps H. v. Meyer. Side view of skull. Muschelkalk; Bayreuth. *A*, orbit; *N*, external narial opening. $^1/_3$ nat. size (after H. von Meyer).

compressed snout; the hinder border of the squamosals bearing small dermal tubercles. Premaxillae and symphysis of lower jaw toothless, probably covered in life by a horny sheath. Palatine with two, maxilla with three, dentary with two crushing teeth. Trunk short and broad. Dermal armour of

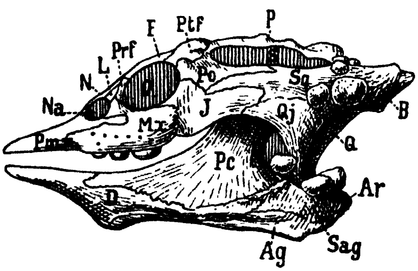


Fig. 390.
Placochelys placodonta Jaekel. Left side view of skull and mandible. Lower Keuper; Hungary. *B*, bony bosses; *N*, nasal; *Na*, narial opening; *O*, orbit; *Qj*, quadrato-jugal; *S*. temporal fossa; other letters as in Fig. 367. $^1/_3$ nat. size (after Jaekel).

Fig. 391.
Psephoderma alpina H. v. Meyer. Dermal armour. Rhaetic; Ruhpolding, Bavaria. $^1/_4$ nat. size (after H. v. Meyer).

conical bony tubercles, variable in size, closely pressed together, forming both a dorsal and a ventral shield. *P. placodonta* Jaekel, with skull about 15 cm. in length. Lower Keuper; Vesprem, Plattensee, Hungary. Species also in Rhaetic of Bavarian Alps.

Paraplacodus Peyer. M. Trias; Tessin, Switzerland.

Psephosaurus E. Fraas. Dermal shield. Lettenkohle; Würtemberg.

Saurosphargis Volz. Lower Muschelkalk; Silesia.

Psephoderma H. v. Meyer (Fig. 391). Dermal shield of polygonal plates. *P. alpinum* H. v. Meyer. Rhaetic; Bavaria. Perhaps also in Lettenkohle of Würtemberg, Triassic of Lombardy, and Rhaetic of Aust Cliff, England.

Order 7. SAUROPTERYGIA.

Primitive aquatic reptiles with short tail, swimming with large paddle-shaped paired limbs. Roofing bones of temporal region of skull contracting into a single broad arch; quadrate fixed. External nares separate, just in advance of the orbits;

a large pineal foramen; vomer paired; pterygoids meeting extensively along the middle line. Teeth conical, in separate sockets, in single series along margin of jaws. Vertebrae amphiplatyan; sacrum composed of two to six vertebrae. Cervical ribs articulating only with centra, never with their arches; dorsal ribs single-headed, articulating only with neural arches; abdominal ribs present between the robust limb arches. Scapulae with ventral extension; coracoids large and in contact; no ossified sternum. Limbs more or less paddle-shaped, with five digits which are usually elongated with supernumerary phalanges. No dermal armour.

The Sauropterygians range from the Trias of Europe and Asia to the Upper Cretaceous of many parts of the world. The earlier forms are mostly small amphibious animals with slender, elongated limbs; the later forms are comparatively large (even 13 metres in length) and completely adapted for marine life. Some may have existed in freshwaters, and a few are known to have frequented estuaries, but the majority must have lived in shallow seas and the open ocean. Their stomach contents show that they fed chiefly on fishes or small reptiles, cuttle-fishes and other molluscs. Like the existing crocodiles, they swallowed stones to assist digestion (gastroliths).[1]

The Sauropterygians evidently evolved from land animals, and the imperfectly known *Trachelosaurus* Broili, from the Bunter Sandstone of Bernburg, may be one of the links. In this genus the neural arches are fused with the centra in the cervical and anterior dorsal vertebrae, and the ilium is that of a land animal. The neck is much elongated. The Triassic *Tanystropheus* H. von Meyer (see p. 270) and *Askeptosaurus* Nopcsa may be other links.

Sub-Order 1. NOTHOSAURIA.[2]

Crawling or swimming reptiles. Scapulae well separated by a stout clavicular arch. The three pelvic bones entering the acetabulum. Humerus with entepicondylar foramen or groove; radius and ulna (tibia and fibula) elongated but shorter than the humerus (femur); the five digits with normal number of phalanges and apparently claws. Feet probably webbed only.

Family 1. Nothosauridae.

No vacuity between pterygoid bones in palate; teeth sometimes on palate. Neck elongated. Coracoids not much extended along their median symphysis. Limbs comparatively slender, of nearly equal size. Triassic.

Nothosaurus Münster (Figs. 392-395). The skull (Fig. 392) is elongated and somewhat contracted anteriorly, 35 cm. to 1 m. long. The supratemporal vacuities are very large, the unpaired parietal being reduced to a narrow bar,

[1] *Brown, B.*, Science, n.s., vol. xix., p. 184, 1904.—*Janensch, W.*, Ein Plesiosaurier-Rest mit Magensteinen. Sitzb. Ges. naturf. Freunde, Berlin, 1928, p. 89.—*Wiman, C.*, Blocktransport genom Saurier. Geol. Fören. Förhandl., vol. xxxviii., p. 369, 1916.

[2] *Arthaber, G. von*, Phylogenie der Nothosaurier. Acta Zoologica, vol. v., p. 439, 1924.—*Boulenger, G. A.*, *Lariosaurus*. Trans. Zool. Soc. Lond., vol. xiv., p. 1, 1896.—*Broili, F.*, Sauropterygier [*Rhäticonia*] aus den Arlbergschichten. Sitzb. Bayer. Akad. Wiss., math.-naturw., Abth., 1927, p. 205.—*Broili, F.*, and *Fischer, E.*, *Trachelosaurus fischeri*. Jahrb. k. preuss. geol. Landesanst. Berlin, vol. xxxvii., p. 359, 1917.—*Dames, W.*, *Anarosaurus pumilio*. Zeitschr. Deutsch. Geol. Ges., vol. xlii., p. 74, 1890.—*Deecke, W.*, *Lariosaurus* und einige andere Saurier der lombardischen Trias. Zeitschr. Deutsch. Geol. Ges., vol. xxxviii., p. 170, 1886.—*Edinger, T.*, *Nothosaurus*. 1. Schädelhöhle. Senckenbergiana, vol. iii., p. 121, 1921.—2. Gaumenfrage. *Loc. cit.*, p. 193, 1921.—3. Schädelfund im Keuper. *Loc. cit.*, vol. iv., p. 37, 1922.—*Fritsch, K. von*, Saurier des Halle'schen unteren Muschelkalkes. Abhandl. Naturf. Ges. Halle, vol. xx., p. 271, 1894.—*Geissler, G.*, Neue Saurierfunde aus dem Muschelkalke von Bayreuth. Zeitschr. Deutsch.

pierced posteriorly by a pineal foramen. The orbits are oval, relatively small, and placed slightly in front of the middle; not far removed from them are the external nares. The unpaired frontal is much elongated, the premaxillae only moderately so, and the prefrontals are small and triangular.

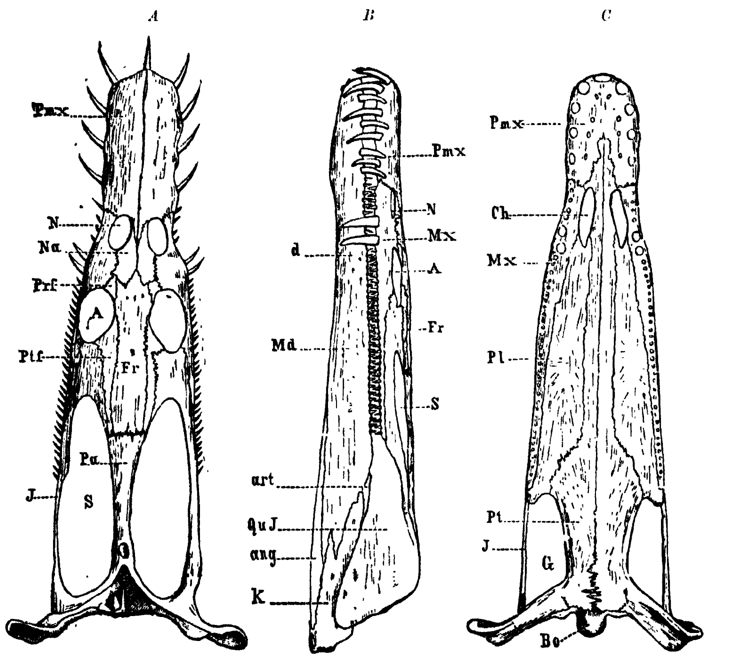


Fig. 392.

Nothosaurus mirabilis Münster. Skull, slightly restored, 1/4. Muschelkalk; Bayreuth, Germany. *A*, Dorsal aspect (after Quenstedt). *B*, Lateral aspect. *C*, Palatal aspect (after v. Meyer). *D*, Tooth, nat. size. *A*, orbit; *ang*, angular; *art*, surangular; *Bo*, basioccipital condyle; *Ch*, internal nares; *d*, dentary; *Fr*, frontal; *G*, infratemporal vacuity; *J*, jugal; *k*, articular; *Md*, mandible; *Mx*, maxilla; *N*, external narial opening; *Na*, nasal; *Pa*, parietal; *Pl*, palatine; *Pmx*, premaxilla; *Prf*, prefrontal; *Pt*, pterygoid, bounded in front by vomer (suture not shown); *Ptf*, postfrontal; *QuJ*, quadrato-jugal fused with squamosal and supratemporal; *S*, supratemporal vacuity.

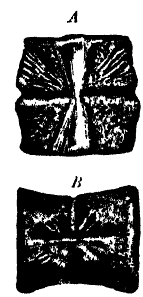


Fig. 393.

Cervical vertebra, nat. size, of species shown in Fig. 392. *A*, *B*, Dorsal and lateral aspects.

The long and narrow maxillae unite posteriorly with a slender jugal, which enters into the temporal arch. Pterygoids and palatines are strongly developed, without teeth; there are no suborbital vacuities; the internal

Geol. Ges., vol. xlvii., p. 331, 1895.—*Gürich, G.*, Einige Saurier des oberschlesischen Muschelkalkes. Zeitschr. Deutsch. Geol. Ges., vol. xxxvi., p. 125, 1884.—*Dactylosaurus*. *Loc. cit.*, vol. xxxviii., p. 457, 1886.—*Huene, F. von*, *Simosaurus*. Zeitschr. f. Abstamm. u. Vererbungslehre, vol. xxiii., p. 206, 1920, and Acta Zoologica, 1921, p. 201.—*Jaekel, O.*, Schädelbau der Nothosauriden. Sitzungsb. Ges. naturf. Freunde, Berlin, 1905, p. 60.—*Koken, E.*, *Nothosaurus*. Zeitschr. Deutsch. Geol. Ges., vol. xlv., p. 337, 1893.—*Kunisch, H.*, Saurierplatte aus dem oberschlesischen Muschelkalk. Zeitschr. Deutsch. Geol. Ges., vol. xl., p. 671, 1888.—*Meyer, H. von*, Fauna der Vorwelt, vol. ii., 1847-55.—*Nopcsa, F.*, Some Nothosaurian Reptiles from the Trias. Geologica Hungarica, Ser. Palaeont., vol. i., p. 20, 1928.—*Peyer, B.*, *Ceresiosaurus*. Abh. Schweiz. Palaeont. Ges., vol. li., 1931.—*Pachypleurosaurus*. *Loc. cit.*, vol. lii., 1932.—*Schrammen, A.*, Nothosauriden des unteren Muschelkalkes in Oberschlesien. Zeitschr. Deutsch. Geol. Ges., vol. li., p. 388, 1899. —*Schroeder, H.*, Wirbeltiere der Rüdersdorfer Trias. Abhandl. k. preuss. geol. Landesanst., n. f., pt. 65, 1914.—*Schuster, J.*, and *Bloch, R.*, Unterkiefer von *Nothosaurus raabi*. Centralbl. f. Min., etc., 1925, Abt. B, p. 60.—*Seeley, H. G.*, *Neusticosaurus pusillus* Fraas. Quart. Journ. Geol. Soc., vol. xxxviii., p. 350, 1882.—*Volz, W.*, *Proneusticosaurus*. Palaeontogr., vol. xlix., p. 120, 1902.

nares are placed far forwards on either side of the paired vomer. A single series of conical, slightly curved, and striated teeth (Fig. 392, *D*) is borne by the maxillae, premaxillae, and dentary. All of the rostral and one or two of the anterior maxillary teeth are considerably enlarged.

Owing to the sutural union between the vertebral centra and their neural

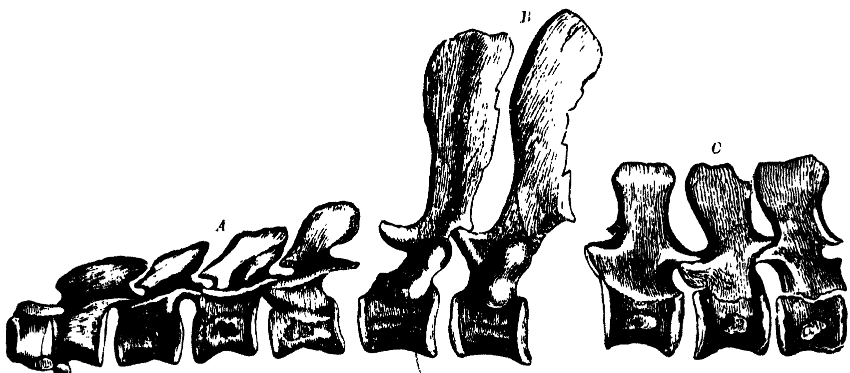


Fig. 394.

Nothosaurus mirabilis Münster. *A*, The five anterior cervicals. *B*, Two dorsals. *C*, Three caudal vertebrae. Muschelkalk; Bayreuth. 1/2 nat. size (after H. von Meyer).

arches, the former are usually found detached in the fossil state, and exhibit a cruciform impression on the dorsal surface (Fig. 393). There are about twenty cervicals (Fig. 394), all of which, excepting atlas and axis, bear short, curved, double-headed ribs. In the trunk region the neural spines are more strongly developed, with transverse processes and small zygapophyses. The sacrum is unknown. The caudal vertebrae have single-headed ribs attached to their centra, and also small chevron bones. The abdominal ribs comprise a median longitudinal series sharply bent in the middle line, and a paired lateral series.

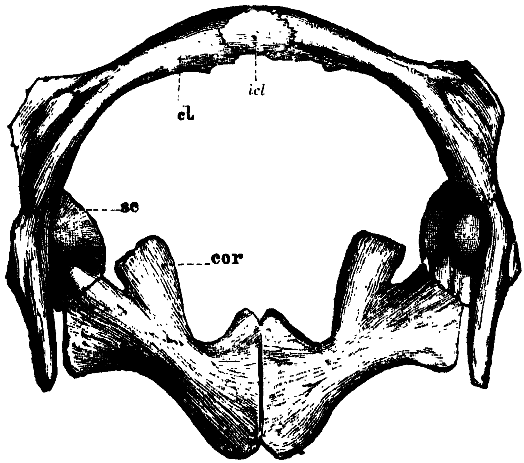


Fig. 395.

Nothosaurus mirabilis Münster. Dorsal aspect of pectoral arch. Muschelkalk; Bayreuth. *cl*, clavicle; *cor*, coracoid; *icl*, interclavicle; *sc*, scapula. 1/3 nat. size.

In the pectoral arch (Fig. 395) the clavicles (*cl*) are well developed, and form a regular arch into which a small, oval interclavicle (*icl*) enters. The ends of the clavicular arch are suturally united with a pair of stout scapulae, which have oblique dorsal processes. The coracoids are not much extended in the median line, and their antero-internal margin is notched and incomplete; apparently they were capped by

cartilage. The humerus is moderately long, curved, and very robust; it is pierced distally by an entepicondylar foramen. Radius, ulna, and metacarpals are likewise rather long and slender, the paddle-shaped form of limb being not yet fully acquired.

The bones of the pelvic arch are robust, and, owing to their loose articulation, usually occur detached in the fossil state. The ilium is very short and stout, somewhat expanded distally, and provided with two articular facets. Pubis and ischium are both of large size, narrowed and thickened at the acetabulum, and distally expanded; a small ischio-pubic fenestra in the pelvis. The femur is longer and more slender than the humerus, nearly straight, moderately thickened at the extremities, and with rounded articular faces. The remaining bones of the hind limb are imperfectly known.

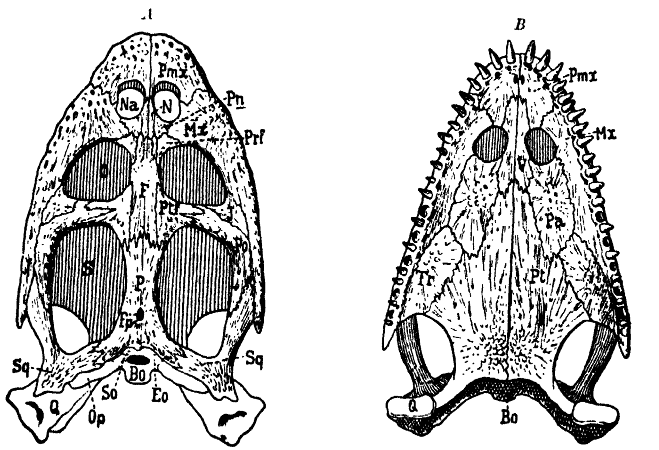


FIG. 396.

Simosaurus gaillardoti H. von Meyer. Skull from above (*A*) and in palatal aspect (*B*). Upper Muschelkalk; Crailsheim, Würtemberg. *Bo*, basioccipital; *Eo*, exoccipital; *F*, frontal; *Fp*, pineal foramen; *J*, jugal; *Mx*, maxilla; *N*, nasal; *Na*, external narial opening; *O*, orbit; *Op*, opisthotic; *P*, parietal; *Pa*, palatine; *Pmx*, premaxilla; *Pn*, postnasal or adlachrymal; *Po*, postorbital; *Prf*, lachrymal or prefrontal; *Pt*, pterygoid; *Ptf*, postfrontal; *Q*, quadrate; *S*, temporal fossa; *So*, supraoccipital; *Sq*, squamosal; *Tr*, transverse; *V*, vomer. $^1/_6$ nat. size (after Jaekel). See also figs. by F. von Huene, Acta Zoologica, 1921, pp. 205, 207, etc.

Nothosaurus is an exclusively Triassic genus, and occurs most abundantly in the Muschelkalk of Southern Germany. *N. mirabilis* Münster is the typical and best-known species, attaining a length of 3 m. Smaller species are found in the Buntsandstein and Lettenkohle. A single Nothosaurian humerus is known from the Trias near the Dead Sea in Trans-Jordania (C. W. Andrews, Ann. Mag. Nat. Hist. [9], vol. xiv., p. 89, 1924). *Germanosaurus* Nopcsa (*Eurysaurus* Frech *nec* Gaudry) seems to have paired frontal bones, but otherwise resembles *Nothosaurus*.

Lamprosaurus, *Opeosaurus*, *Conchiosaurus* v. Meyer. Muschelkalk.

Simosaurus v. Meyer (Fig. 396). Skull broad and depressed, with obtuse snout. Teeth short, obtusely conical or clavate, the crown strongly striated. Upper Muschelkalk and Lettenkohle.

Pistosaurus v. Meyer. Known only by the skull, which tapers anteriorly, and attains a length of 35 cm. Premaxillae elongate and slender, the small narial openings placed between them and the maxillae. Nasals greatly

reduced and displaced posteriorly. Palate with an unpaired vacuity between the premaxillae. Muschelkalk; Franconia and Silesia.

Dactylosaurus Gürich, *Anarosaurus* Dames, *Cymatosaurus* K. v. Fritsch, *Proneusticosaurus* Volz (*Dolichovertebra* v. Huene). Muschelkalk; Silesia, Saxony, and Thuringia.

Pachypleurosaurus Broili (*Pachypleura* Cornalia). About sixteen cervical vertebrae, twenty dorsals, three sacrals, and nearly forty caudals. *P. edwardsi* Corn., about 40 cm. long. Middle Trias; Besano, Lombardy, and Tessin, Switzerland.

Neusticosaurus Seeley. Resembling *Pachypleurosaurus*, but with more slender trunk, shorter tail, and more slender femur. *N. pusillus* Fraas sp. Lettenkohle (Upper Triassic); Hoheneck.

Macromerosaurus Curioni. Middle Triassic; Perledo.

Rhaeticonia Broili. Premaxillary teeth relatively large and bent outwards; length of skull exceeding half that of the neck. About eighteen cervical, twenty-one dorsal, and thirty caudal vertebrae. Ribs much thickened. *R. rothpletzi* Broili, about 30 cm. long. Middle Triassic; Vorarlberg.

Partanosaurus, *Microleptosaurus* Skuphos. Middle Triassic; Vorarlberg. *Ceresiosaurus* Peyer. Triassic; Switzerland.

Lariosaurus Curioni (Fig. 397). Body lizard-like, tail forming about one-third the total length. There are about twenty cervical vertebrae, over twenty dorsals, five sacrals, and over forty caudals. Cervical ribs small and double-headed; dorsal ribs very robust. A median longitudinal and two paired lateral series of abdominal ribs. Two large proximal carpals and tarsals, the distal five each supporting a digit. Phalangeal formula of hand, 2, 3, 4, 4, 3. Hind limb longer and stouter than the anterior, but otherwise very similar; phalangeal formula 2, 3, 4, 5, 4. Palate with suborbital and infratemporal vacuities; a row of teeth on the pterygoid. *L. balsami* Cur. (Fig. 397), nearly a metre in length. Middle Triassic; Perledo, Lake Como, Italy.

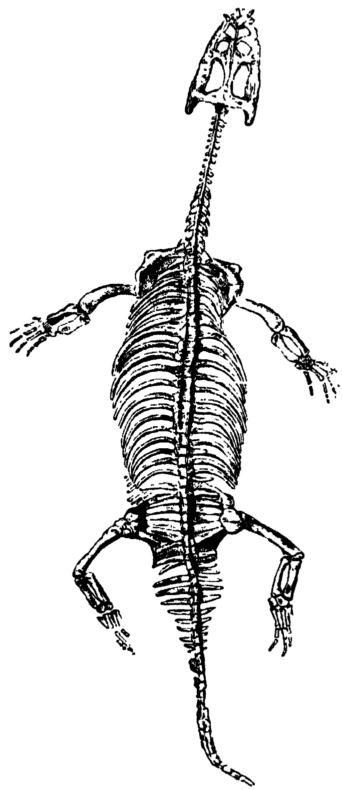


FIG. 397.
Lariosaurus balsami Curioni. Skeleton, dorsal aspect. Muschelkalk; Perledo on Lake Como, Lombardy. $^1/_{10}$ nat. size.

Phygosaurus v. Arthaber. Resembling *Lariosaurus*, but more slender trunk with less thickened ribs and only three sacral vertebrae. *P. perledicus* v. Arth., about 75 cm. in length. Middle Triassic; Perledo.

Psilotrachelosaurus Nopcsa. Middle Triassic; Töplitsch, Austria.

Pontopus Nopcsa. Footprints showing web between toes. Keuper; Cheshire.

Sub-Order 2. PLESIOSAURIA.[1]

Swimming reptiles. Interpterygoid vacuity or vacuities in palate. Scapulae with the ventral extensions tending to replace the clavicular arch. Ilium displaced backwards, articulating only with ischium. Humerus without entepicondylar foramen; radius and ulna (tibia and fibula) much shortened; the five digits elongated by supernumerary phalanges and united in a paddle.

A peculiar pyritous concretion from the Upper Lias of Whitby is interpreted by Seeley as a mass of embryos of a Plesiosaur, indicating that these reptiles were viviparous.

Family 1. Plesiosauridae.

Head small; neck elongated; cervical ribs stout and double-headed. Clavicular arch tending to diminish in size as the scapulae increase, the latter sometimes becoming fused with each other and the coracoids in the median line. Coracoids much extended along median symphysis. Radius and ulna (tibia and fibula) longer than broad. Fore limb at least as large as hind limb. Upper Triassic and Lower Jurassic.

Plesiosaurus Conybeare (Figs. 398-400). Head small, neck very long. Snout not elongated, orbits elliptical and placed near the middle of the

[1] *Andrews, C. W.*, Development of the Shoulder-girdle of a Plesiosaur (*Cryptocleidus oxoniensis*). Ann. Mag. Nat. Hist. [6], vol. xv., p. 333, 1895.—Skull in *Peloneustes philarchus*. *Loc. cit.*, vol. xvi., p. 242, 1895.—Plesiosaurian Skull. Quart. Journ. Geol. Soc., vol. lii., p. 246, 1896.—Skull of a Pliosaur. *Loc. cit.*, vol. liii., p. 177, 1897.—Skeleton of *Peloneustes philarchus*. Geol. Mag. [5], vol. vii., p. 110, 1910.—New Plesiosaur (*Plesiosaurus capensis* sp. nov.) from the Uitenhage Beds of Cape Colony. Ann. S. African Mus., vol. vii., p. 309, 1911.—Catalogue of Marine Reptiles of Oxford Clay, Brit. Mus., pts. i. ii., 1910, 1913.—*Rhomaleosaurus thorntoni* sp. nov. Ann. Mag. Nat. Hist. [9], vol. x., p. 407, 1922.—New Plesiosaur from the Weald Clay. Quart. Journ. Geol. Soc., vol. lxxviii., p. 285, 1922.—*Bogolubow, N. N.*, Plesiosaurians in Russia [in Russian, with bibliography and plates]. Mem. Imp. Univ. Moscow, vol. xxix., 1911.—*Brandes, T.*, Plesiosauriden aus dem unteren Lias von Halberstadt. Palaeontogr., vol. lxi., p. 41, 1914.—*Broili, F.*, Plesiosaurierreste von der Insel Quiriquina. Neues Jahrb. f. Min., etc., Beil.-Bd. lxiii., Abt. B, p. 497, 1930.—*Cope, E. D.*, Structure of the Skull in the Plesiosaurian Reptilia. Proc. Amer. Phil. Soc., 1894, p. 109.—*Dames, W.*, Plesiosaurier der süddeutschen Liasformation. Abhandl. k. preuss. Akad. Wiss., Jahr 1895, p. 1, 1896.—*Deecke, W.*, Saurierreste aus den Quiriquina-Schichten in Chile. Neues Jahrb. f. Min., etc., Beil.-Bd. x., p. 32, 1895.—*Fraas, E.*, Plesiosaurier aus dem oberen Lias von Holzmaden. Palaeontogr., vol. lvii., p. 105, 1910.—*Huene, F. von*, Ein neuer Plesiosaurier aus dem oberen Lias Württembergs. Jahresh. Vereins f. vaterl. Naturk. Württ., vol. 79, p. 1, 1923.—*Hulke, J. W.*, Shoulder Girdle in Ichthyosauria and Sauropterygia. Proc. Roy. Soc., vol. lii., p. 233, 1892.—*Knight, W. C.*, New Jurassic Vertebrates from Wyoming. Amer. Journ. Sci. [4], vol. v., p. 186, 1898.—*Koken, E.*, *Muraenosaurus*. Neues Jahrb. f. Min., etc., 1913, vol. i., p. 101.—*Linder, H.*, *Peloneustes* und *Pliosaurus*. Geol. u. Palaeont. Abhandl., n.f., vol. xi., p. 337, 1913.—*Mehl, M. G.*, American Jurassic Plesiosaurs. Journ. Geol., vol. xx., p. 344, 1912.—*Owen, R.*, Reptilia of the Liassic Formations. Mon. Palaeontograph. Soc., 1865.—Reptilia of the Cretaceous Formations. *Loc. cit.*, 1851-64.—*Riabinin, A.*, Zwei Plesiosaurier aus den Jura- und Kreide-Ablag. Russlands. Mém. Com. Géol. St. Pétersb., n.s., livr. 43, 1908.—*Seeley, H. G.*, Shoulder Girdle and Clavicular Arch in Sauropterygia. Proc. Roy. Soc., vol. li., p. 119, 1892. Also *loc. cit.*, vol. liv., p. 149, 1893.—Pyritous Concretion from Lias of Whitby . . . Embryos of *Plesiosaurus*. Ann. Rep. Yorks. Phil. Soc., 1895, p. 20.—*Smellie, W. R.*, *Apractocleidus teretipes*. Trans. Roy. Soc. Edinb., vol. li., p. 609, 1917.—*Sollas, W. J.*, New Species of *Plesiosaurus* from Lower Lias of Charmouth. Quart. Journ. Geol. Soc., vol. xxxvii., p. 440, 1881.—*Watson, D. M. S.*, Two New Genera of Upper Liassic Plesiosaurs. Mem. and Proc. Manchester Lit. and Phil. Soc., vol. liv., no. 4, 1909. Also *loc. cit.*, no. 11, 1910.—The Elasmosaurid Shoulder-Girdle and Fore-Limb. Proc. Zool. Soc., 1924, p. 885.—*Wegner, T.*, *Brancasaurus brancai*. Branca-Festschrift, Berlin, p. 235, 1914 [Bibliography].—*Williston, S. W.*, North American Plesiosaurs. Part I. Field Columbian Museum, publ. 73, 1903.—*Elasmosaurus*, *Cimoliasaurus*, and *Polycotylus*. Amer. Journ. Sci. [4], vol. xxi., p. 221, 1906.—Skull of *Brachauchenius*, with Observations on the Relationships of the Plesiosaurs. Proc. U.S. Nat. Mus., vol. xxxii., p. 477, 1907.—*Trinacromerum*. Journ. Geol., vol. xvi., p. 715, 1908.

skull, supratemporal vacuities large, irregular. Interpterygoid and suborbital vacuities small. Mandibular symphysis short. Teeth acutely conical, longitudinally grooved; anterior teeth somewhat enlarged. Scapulae separated by a well-developed clavicular arch; interclavicle longer than broad.

The number of cervical vertebrae varies among the different species between thirty and forty. The centra are but slightly biconcave, and united to the neural arches by suture. Except the atlas and axis, all the cervicals bear short, double-headed ribs, attached directly to the centra. There are about twenty dorsal vertebrae with well-developed transverse processes. The two sacral vertebrae are characterised by having somewhat shorter transverse processes and broader ribs than the rest. There are between thirty and forty caudals, most of which bear short, single-headed ribs articulated with their centra, and chevron bones of which the right and left halves do not fuse below. The abdominal ribs are very robust, in a median and three paired lateral series.

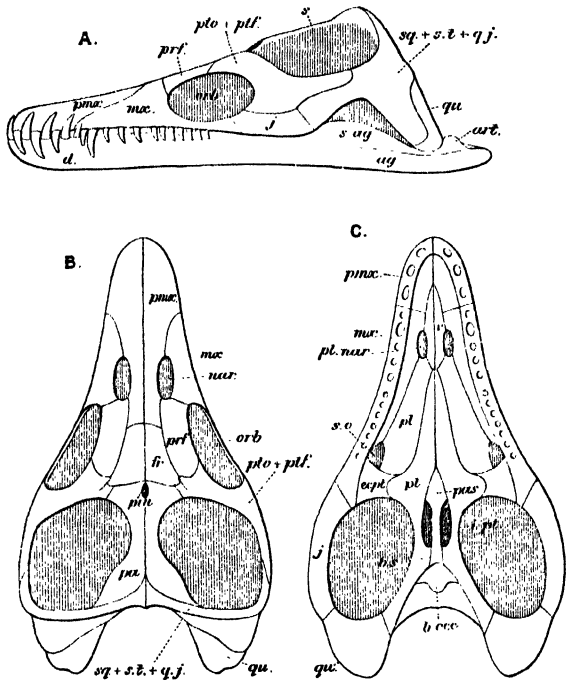


FIG. 398.

Plesiosaurus macrocephalus Owen. *A*, Lateral; *B*, Superior; *C*, Palatal aspects of skull. Lower Lias; Lyme Regis, Dorset. *ag*, angular; *art*, articular; *bocc*, basioccipital; *bs*, basisphenoid; *d*, dentary; *ecpt*, transverse or ectopterygoid; *fr*, frontal; *ipt*, interpterygoid vacuity; *j*, jugal; *mx*, maxilla; *nar*, external narial opening; *orb*, orbit; *pa*, parietal; *pas*, parasphenoid; *pin*, pineal foramen; *pl*, palatine; *pmx*, premaxilla; *prf*, prefrontal; *pt*, pterygoid; *pt. nar*, posterior nares; *ptf*, postfrontal; *pto*, postorbital; *qj*, quadrato-jugal; *qu*, quadrate; *s*, supratemporal vacuity; *sag*, surangular; *so*, suborbital vacuity; *sq*, squamosal; *st*, supratemporal or prosquamosal; *v*, vomer. 1/6 nat. size (from Woodward, after Andrews).

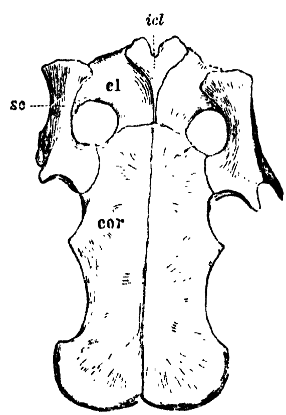


FIG. 399.

Plesiosaurus laticeps Owen. Pectoral arch, ventral aspect. Lower Lias; Dorset. *cl*, clavicle; *cor*, coracoid; *icl*, interclavicle; *sc*, scapula. 1/10 nat. size.

In the pectoral arch (Fig. 399) the coracoids are considerably longer than broad, and joined in a long median symphysis. The clavicular arch, though still showing the limits of the clavicles and interclavicle, is represented by a single, broad, bilaterally symmetrical bone to which the coracoids and scapulae are firmly united. The latter are only slightly extended ventrally underneath the clavicular arch.

The humerus is robust and distally much expanded, but without epicondylar foramen or groove. This bone and the femur are noteworthy as exhibiting large, conical "epiphyses" similar to those of frogs, certain Chelonians, and young pigeons.[1] The radius and ulna are both a little longer than broad. Four elements are usually present in the proximal, and three in the distal row of the carpus; the five constricted metacarpals are similar in form to the phalanges. The phalangeal formula is inconstant, but the third and fourth digits are always the longest, sometimes comprising as many as nine phalanges. The hind limb differs in no respect from the fore, except that it is slightly stouter. The pubes are relatively large, with convex anterior and notched posterior margin, but not pierced by a foramen. They meet, as do also the much smaller ischia, in a long median symphysis. The ilium is slender.

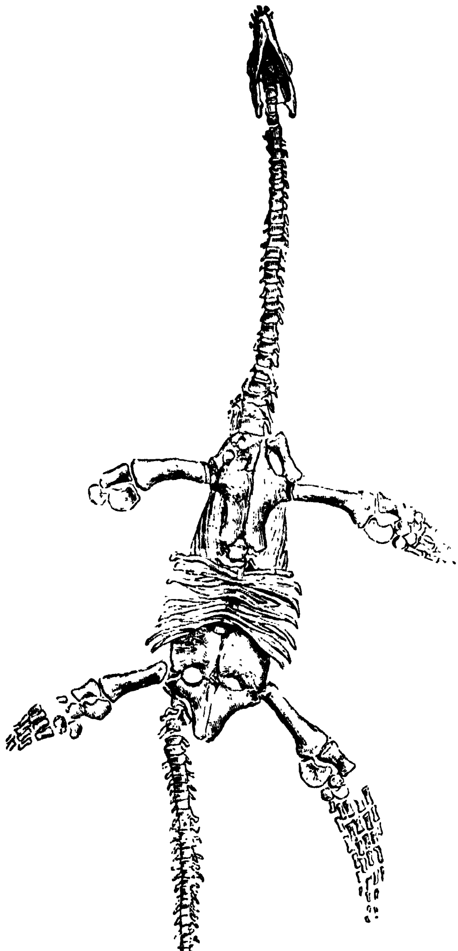


FIG. 400.
Plesiosaurus dolichodeirus Conyb. Skeleton, ventral aspect. Lower Lias; Lyme Regis, Dorset. $^1/_{23}$ nat. size (after Hawkins).

Several nearly perfect skeletons of *Plesiosaurus* are known from the Lower and Upper Lias of England and Germany, and supposed fragments occur in the Muschelkalk, Upper Keuper, and Rhaetic. The typical species, *P. dolichodeirus* Conybeare (Fig. 400), from the Lower Lias of Lyme Regis, England, attains a total length of 3 m. Among other species from the same locality, *P. conybearei* Sollas attains a length of 5 m. Beautiful skeletons are preserved in the British, Berlin, and Stuttgart Museums. *P. guilelmi imperatoris* Dames, from Upper Lias, Holzmaden, Würtemberg, over 3 m. in length.

Eurycleidus Andrews. Stouter neck than in *Plesiosaurus*, and interclavicle broader than long. *E. arcuatus* Owen sp. and *E. megacephalus* Stutchbury sp. Lower Lias; Somerset. *E. victor* Fraas sp., 3·5 m. long. Upper Lias; Holzmaden, Würtemberg.

Eretmosaurus Seeley. Coracoids truncated anteriorly, and not extending in

[1] *Moodie, R. L.*, Reptilian Epiphyses. Amer. Journ. Anat., vol. vii., p. 443, 1908.—*Parsons, F. G.*, On Pressure Epiphyses. Journ. Anat. and Physiol., vol. xxxix., p. 402, 1905.

front of the glenoid cavity for the humerus. Scapulae extending downward and inward so as to become fused with each other and also with coracoids in the median line. Clavicular arch degenerate. *E. rugosus* Owen sp. Lower Lias; England.

Macroplata Swinton. Lower Lias; Warwickshire.

Microcleidus Watson. Much resembling *Eretmosaurus*, but with very high neural spines in dorsal vertebrae. No interclavicle. *M. homalospondylus* Owen sp. Upper Lias; Whitby.

Sthenarosaurus Watson. Upper Lias; Whitby.

Thaumatosaurus H. von Meyer. Indeterminable vertebrae from the Middle Brown Jura of Neuffen, Würtemberg.

Family 2. **Pliosauridae.**

Head large; neck short; cervical ribs stout and mostly double-headed. Scapulae separated by small clavicular arch; coracoids much extended along median symphysis. Pelvis very large. Radius and ulna (tibia and fibula) very short and broad. Fore paddles usually smaller than hind paddles. Jurassic.

Rhomaleosaurus Seeley. About fifteen cervical vertebrae, with base of neural arch extending along whole length of centrum, and zygapophysial facets horizontal. About twenty-five dorsal and four or five sacral vertebrae; sacral ribs very strong, and two articulating closely with the ilium. Humerus larger than femur. Ischium truncated behind. *R. cramptoni* Carte and Baily sp. and *R. thorntoni* Andrews, both 6 or 7 m. in length. English Upper Lias.

FIG. 401.

Pliosaurus grandis Owen. Tooth. Kimmeridgian; Dorset. 1/4 nat. size (after Owen).

Pliosaurus Owen (*Ischyrodon* H. v. Meyer; *Spondylosaurus* Fischer; *Liopleurodon* Sauvage) (Fig. 401). Skull with snout a little elongated and mandibular symphysis extending to about the seventh tooth. Conical teeth (Fig. 401) with the crown bearing numerous vertical ridges, and the root very large with pulp cavity open below. About twenty-three cervical and twenty-four dorsal vertebrae. Bones very dense in young, of loose texture in adult. *P. grandis* Owen. Kimmeridge Clay; England. *P. ferox* Sauvage sp., with skull about 1·5 m. in length. Oxford Clay; England and N. France. Jurassic; Russia.

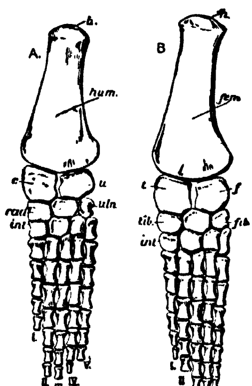


FIG. 402.

Peloneustes philarchus Seeley sp. Fore (*A*) and hind (*B*) paddle. Oxford Clay; Peterborough. *f*, fibula; *fem*, femur; *fib*, fibulare; *h*, head of humerus and femur; *hum*, humerus; *int*, intermedium; *r*, radius; *rad*, radiale; *t*, tibia; *tib*, tibiale; *u*, ulna; *uln*, ulnare. 1/9 nat. size (after Andrews).

Simolestes Andrews. Skull short and broad, mandibular symphysis short. Humerus shorter than femur. *S. vorax* Andrews, with skull 73 cm. in length. Oxford Clay; Peterborough.

Peloneustes Lydekker (Fig. 402). Skull elongated, the premaxillae bearing about six pairs of teeth; mandibular symphysis much elongated with twelve to fifteen pairs of teeth. *P. philarchus* Seeley sp., known by nearly complete skeletons about 3 m. in length from the Oxford Clay, Peterborough.

? *Megalneusaurus* Knight. Largest known Plesiosaurian, the humerus attaining a length of 1 m., or about one-half the length of the entire fore limb, and articulating only with the radius and ulna. The latter bones are polygonal and closely applied against each other and the three proximal carpals. Coracoids produced in front of the glenoid cavity; vertebrae elongated. *M. rex* Knight. Upper Jurassic; Wyoming.

Family 3. **Elasmosauridae.**

Head small; neck elongated, sometimes excessively so; cervical ribs with single head. Scapulae usually meeting in middle line, and clavicular arch then reduced; coracoids much extended along median symphysis. Radius and ulna (tibia and fibula) so much shortened as to resemble carpal and tarsal bones. Middle Jurassic to Upper Cretaceous.

Muraenosaurus Seeley. Head very small, short and broad. Neck of forty-four vertebrae. Interclavicle large, but clavicles reduced; an interscapular foramen. Fore limb a little larger than hind limb, and humerus not much expanded distally. *M. leedsi* Seeley, about 6 m. in length, and other species in the English Oxford Clay. Perhaps also Russia and Wyoming.

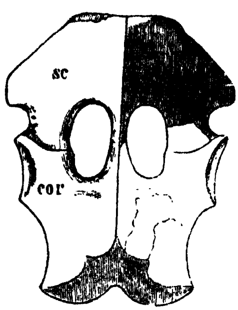


Fig. 403.
Elasmosaurus platyurus Cope. Pectoral arch, shaded parts restored. Upper Cretaceous; Kansas. *cor*, coracoid; *sc*, scapula. Much reduced (after Cope).

Picrocleidus Andrews. Comparatively small species with about forty cervical vertebrae, which are shorter than in *Muraenosaurus*, longer than in *Cryptocleidus*. Small arrow-head shaped interclavicle, rudimentary clavicles. Oxford Clay; Peterborough.

Tricleidus Andrews. Pterygoids with large processes for union with basis cranii. Large broad interclavicle, small clavicles. Humerus articulating distally with radius, ulna, pisiform, and postaxial accessory bone. *T. seeleyi* Andrews, a small species from the Oxford Clay of Peterborough. ? Wyoming.

Cryptocleidus Seeley. Skull about a quarter as long as the neck, which includes about thirty-two vertebrae. Interclavicle rudimentary or absent, clavicles triangular and meeting in median symphysis; no interscapular foramen. Humerus much expanded distally, and articulating with radius, ulna, and postaxial accessory bone. *C. oxoniensis* Phillips sp., 3 m. to 4 m. in length, from English Oxford Clay. *C. simbirskensis* Bogolubow. Callovian; Simbirsk, Russia. *Apractocleidus* Smellie is essentially similar.

Colymbosaurus Seeley. Kimmeridge Clay; Ely.

Leptocleidus Andrews. A small probably freshwater Elasmosaurian with relatively large clavicular arch, the interclavicle broad. Humerus articulating only with radius and ulna. Hard discs between vertebrae at base of neck. *L. superstes* Andrews. Wealden; Sussex. *Plesiosaurus capensis* Andrews, represented by a skull, vertebrae, and some limb-bones from the Uitenhage Beds of Cape Colony, belongs to an allied genus.

Brancasaurus Wegner. Wealden; Westphalia.

Elasmosaurus Cope (Fig. 403). Neck very long and slender, with about seventy vertebrae; neural arches fused with centra. *E. platyurus* Cope, about

13 m. long, from Upper Cretaceous, Kansas. Probably other species also in Russia, Australia, and New Zealand.

Fragments from the Cretaceous of North and South America, Europe, and New Zealand have been named *Cimoliasaurus, Discosaurus, Brimosaurus, Piratosaurus, Oligosimus* Leidy, *Taphrosaurus, Uronautes, Orophosaurus, Piptomerus, Embaphias* Cope, and *Mauisaurus* Hector. Also undetermined fragments in the Cretaceous of Japan.

Family 4. **Polycotylidae**.

Head large, at least as long as neck; cervical ribs with single head. Scapulae separated by clavicular arch. Pelvis large, with elongated ischia. Radius and ulna (tibia and fibula) very short. Upper Cretaceous.

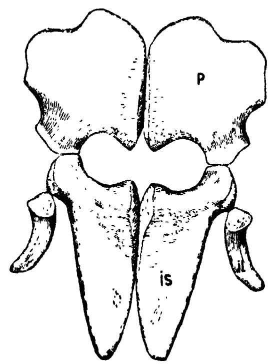


FIG. 404.

Trinacromerum osborni Williston. Pelvis, from below. Upper Cretaceous; Kansas. *il*, ilium; *is*, ischium; *p*, pubis. Much reduced (after Williston).

Trinacromerum Cragin (*Dolichorhynchops* Williston) (Fig. 404). Head long, snout very slender; mandibular symphysis much elongated; teeth small, numerous, uniform; posterior nares small, included between vomer and palatines; pterygoids contiguous only at extremities. Neck shorter than head; axis with ribs; nineteen cervicals and about thirty dorsals. Humerus and femur moderately expanded; three propodials. Known by a nearly complete skeleton about 3 m. in length from the Niobrara Cretaceous of Kansas.

Polycotylus Cope. Over twenty cervical vertebrae and about thirty dorsals, much resembling *Trinacromerum*. Kansas.

Brachauchenius Williston; *Ogmodirus* Williston and Moodie. Cretaceous; Kansas. *Leurospondylus* Brown. Edmonton Cretaceous; Alberta, Canada. *Kronosaurus* Longman. Lower Cretaceous; Queensland.

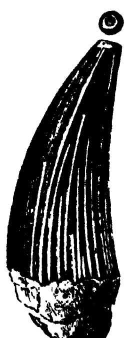


FIG. 405.

Polyptychodon interruptus Owen. Tooth, nat. size. Cenomanian; Kelheim, Bavaria.

Polyptychodon Owen (Fig. 405). Imperfectly known, teeth resembling those of *Pliosaurus*, but with more prominent coronal ridges, some of which extend to the apex. Upper Cretaceous; England, Germany, and Russia.

Order 8. CHELONIA. (*Testudinata.*)[1]

Cranial roof primitively continuous over temporal region, but this region often more or less exposed by emargination of roof from behind or from the outer lateral

[1] *Ammon, L. von*, Schildkröten aus dem Regensburger Braunkohlenton. 12. Jahresb. naturwiss. Ver. Regensburg, p. 1, 1911.—*Baur, G.*, Osteologische Notizen über Reptilien. Zool. Anz., vol. ix., p. 733, 1886.—*Loc. cit.*, vol. xi., pp. 417, 592, 1888; and vol. xii., p. 40, 1889.—Notes on some little known American fossil Tortoises. Proc. Acad. Nat. Sci. Philadelphia, p. 411, 1891.—Bemerkungen über die Phylogenie der Schildkröten. Anat. Anz., vol. xii., p. 561, 1896.—*Boulenger, G. A.*, Catalogue of Chelonians in the British Museum. London, 1889.—*Coker, R. E.*, Diversity in the Scutes of Chelonia. Journ. Morphol., vol. xxi., p. 1, 1910.—*Cope, E. D.*, The Reptiles of the American Eocene. Amer. Nat., vol. xvi., p. 979, 1882.—*Loc. cit.*, vol. xxx., p. 398, 1896.—*Dacqué, E.*, Die fossilen Schildkröten Ägyptens. Geol. u. Palaeont. Abhandl., n.s., vol. x., p. 275, 1912.—

edge; no postparietal or tabular bones. Narial opening usually single; no pineal foramen. Jaws toothless, with horny sheath; palate toothless [except in one known early genus]. Trunk short and broad, encased in bony plates which include expansions of the ribs and abdominal ribs. Ribs inserted intervertebrally. Pectoral and pelvic arches within the bony shell; no separate precoracoid; pelvis with large ischio-pubic fenestra including the passage for the obturator nerve; acetabulum not perforate. Limbs with five digits, and phalanges in terrestrial forms reduced at least to 2, 3, 3, 3, 3.

The Chelonians, or tortoises and turtles, form a homogeneous and narrowly circumscribed group, widely separated from all other reptiles. They first appear in the Upper Keuper of Southern Germany, exhibiting all the typical characters of the Order; and they do not undergo any noteworthy modifications in structure during all their subsequent history. They seem to have been originally dwellers on land, and Eberhard Fraas has suggested that their armour arose as an adaptation to burrowing habits, like that of certain Edentate Mammals. They are now generally regarded as most nearly related to the *Cotylosauria*.

Dames, W., Die Chelonier der norddeutschen Tertiärformation. Palaeont. Abhandl. Dames und Kayser, vol. vi., p. 197, 1894.—*Gilmore, C. W.*, Two new Species of Fossil Turtles from the Lance Formation of Wyoming. Proc. U.S. Nat. Mus., vol. 50, p. 641, 1916.—New Fossil Turtles. *Loc. cit.*, vol. 56, p. 113, 1919.—Fossil Turtles from Pleistocene of Florida. *Loc. cit.*, vol. 71, p. 1, 1927.—Reptilian Faunas of the Torrejon, etc., Formations, New Mexico. U.S. Geol. Surv., Professional Paper 119, 1919.—*Gray, J. E.*, Notes on the families and genera of Tortoises. Proc. Zool. Soc., vol. xxxvii., p. 165, 1869.—*Hay, O. P.*, Fossil Turtles of North America, Carnegie Inst. Publ. no. 75, 1908. Supplemented in Proc. U.S. Nat. Mus., vol. 35, p. 161, 1908; vol. 36, p. 191, 1909; vol. 38, p. 307, 1910; and in 8th Ann. Rep. Florida State Geol. Surv., p. 45, 1916.—Phylogeny of the Shell of the Testudinata and the Relationships of *Dermochelys*. Journ. Morphol., vol. xxxvi., p. 421, 1922.—Shell of *Chelys* and Armor of Turtles in general. Proc. U.S. Nat. Mus., vol. 73, art. 3, 1928.—*Hoffmann, C. K.*, Chelonia, in Bronn's Classen und Ordnungen des Thierreichs, vol. vi., 1879.—*Knowlton, F. H.*, Fossil Turtles accredited to the Judith River Formation. Proc. Washington Acad. Sci., vol. xiii., p. 51, 1911.—*Laube, G. C.*, Schildkröten aus der böhmischen Braunkohlenformation. Abhandl. "Lotos," vol. i., p. 1, 1896, and vol. ii., p. 37, 1900.—*Lydekker, R.*, Siwalik and Narbada Chelonia. Palaeont. Indica, ser. x., vol. iii., 1886.—Catalogue of the Fossil Reptilia and Amphibia in the British Museum, pt. iii. London, 1889.—*Maack, G. A.*, Die bis jetzt bekannten fossilen Schildkröten, etc. Palaeontogr., vol. xviii., 1869.—*Meyer, H. von*, Zur Fauna der Vorwelt, pts. i. and iv. Frankfort, 1845-60.—*Owen, R.*, and *Bell, R.*, Monograph of the fossil Reptilia of the London Clay, pt. i. (Palaeont. Soc.), 1851.—*Owen, R.*, Monograph of the Wealden Chelonia, etc., *loc. cit.*, 1852-53.—*Pictet, F. J.*, and *Humbert, A.*, Monographie des Cheloniens de la Molasse Suisse. Geneva, 1856.—*Portis, A.*, Über fossile Schildkröten aus dem Kimmeridge von Hannover. Palaeontogr., vol. xxv., p. 125, 1878.—Les Cheloniens de la Molasse Vaudoise. Mém. Soc. Paléont. Suisse, vol. ix., 1882.—*Reinach, A. v.*, Schildkrötenreste im Mainzer Tertiärbecken, etc. Abhandl. Senckenb. Naturf. Ges., vol. xxviii., 1900.—Schildkrötenreste aus dem ägyptischen Tertiär. *Loc. cit.*, vol. xxix., p. 1, 1903.—*Ruckes, H.*, Studies in Chelonian Osteology, II. Ann. New York Acad. Sci., vol. xxxi., p. 81, 1929.—*Rütimeyer, L.*, Die fossilen Schildkröten von Solothurn. Denkschr. Schweiz. Naturf. Gesellsch., vol. xxii., 1867; and *loc. cit.*, vol. xxv., 1873.—Über den Bau von Schale und Schädel bei lebenden und fossilen Schildkröten. Verhandl. Naturf. Gesellsch. Basel, vol. iii., p. 255, 1872.—*Sacco, F.*, Cheloni Astiani del Piemonte. Mem. Accad. Torino, vol. xxxix., 1889.—*Siebenrock, F.*, Synopsis der rezenten Schildkröten. Zool. Jahrbücher, Suppl. 10, Heft 3, 1909.—*Stefano, G. de*, Cheloniani fossili cenozoici. Boll. Soc. Geol. Ital., vol. xxi., p. 263, 1902.—Nuovi rettili degli strati a fosfato della Tunisia. *Loc. cit.*, vol. xxii., p. 51, 1903.—*Versluys, J.*, Phylogeny of the Carapace, and on the Affinities of the Leathery Turtle, *Dermochelys coriacea*. Rep. British Assoc. (Birmingham, 1913), p. 791, 1914 (German edition in Palaeont. Zeitschr., vol. i., p. 321, 1914).—*Wagner, J. A.*, Schildkröten und Saurier aus den lithographischen Schiefer. Abhandl. Bayer. Akad. Wissensch., II. Classe, vol. vii., p. 291, 1853; and *loc. cit.*, vol. ix., p. 68, 1861.—*Wieland, G. R.*, Evolution of the Testudinate Humerus. Amer. Journ. Sci., vol. ix., p. 413, 1900.—*Wiman, C.*, Fossile Schildkröten aus China. Palaeont. Sinica, ser. C, vol. vi., fasc. 3, 1930 [see also *Nopcsa, F.*, Zur systematischen Stellung dreier von Wiman aus China beschriebener fossiler Schildkröten. Centralbl. f. Min., etc., 1930, Abt. B, p. 510].—*Zdansky, O.*, Über die Temporalregion des Schildkrötenschädels. Bull. Geol. Inst. Upsala, vol. xix., p. 89, 1924.

The most distinctive character of the group is the investment of the body in a more or less rigid shell or box, which is composed partly of the modified neural spines and ribs, and partly of dermal ossifications more or less intimately united with the former. Into this shell the limbs, tail, and usually also the neck and head are capable of being retracted.

In most forms both the dorsal shell or *carapace*, and the ventral or *plastron*, are superficially covered with a horny epidermal layer, which is divided by indented sutures into a few large scutes or *shields*. These epidermal shields are arranged independently of the subjacent bony plates, and are wanting only in *Trionychoidea* and *Dermochelyidae*. They afford valuable diagnostic characters among Recent forms, but as a rule are completely destroyed in fossilisation, their sutures being merely indicated by shallow sulci on the bony plates. On the carapace they form a median dorsal and a paired lateral series, there being usually five unpaired or *vertebral shields*, and four or five pairs of *costal shields* (Figs. 411, 413, 415, 418). Round the periphery there is also a series of about twenty-four *marginals* (*marginalia*), the anterior of which is called the *nuchal*, and the posterior, sometimes double, the *caudal* or *supracaudal* shield. In the primitive Triassic forms there are some supplementary shields between the costals and marginals. Five or six pairs of epidermal shields are present in the plastron, but there is no median series. The anterior pair is that of the *gulars*, following which in the order named are the *humerals*, *pectorals*, *abdominals*, *femorals*, and *anals*. Occasionally the gulars are separated in front by a single or double *intergular* shield. There are also sometimes *inguinal* shields on the bridge between the carapace and plastron.

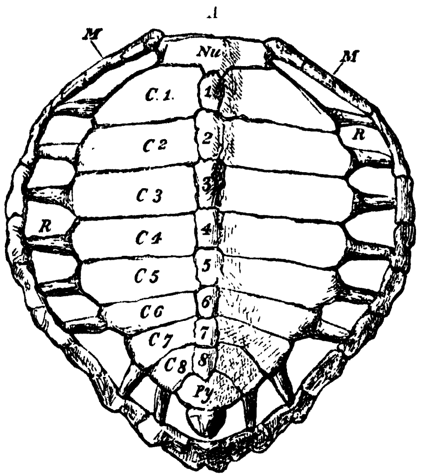
The bony plates of the *carapace* (Fig. 406, *A*, *B*) are formed partly by lateral expansions of the spinous processes of eight dorsal vertebrae (second to ninth), and of the ribs belonging to these vertebrae; and in still greater part by dermal ossifications overlying the ribs and joining the expanded spinous processes on either side of the median line. The plates of the carapace thus differ in number and arrangement from the epidermal shields, inasmuch as they coincide with the vertebrae and ribs. The latter retain their individuality more or less distinctly on the visceral side of the costal bones, and extend across the vacuities when the carapace is incomplete.

The median series of eight bony plates in the carapace are called *neurals* or *vertebrals*; and the lateral pieces lying superjacent to the ribs, which are firmly united to one another and to the neurals by suture, are termed *costals* or *pleurals*. Sometimes not all of the neural bones are developed, and among the recent *Pleurodira* of Australia they are wanting altogether. In front of the series of neural plates is a large hexagonal plate, the *nuchal*, which is broader than long, and situated above the first dorsal vertebra. This plate, which is present in all Chelonians, is a dermal bone. Continuing the series of neurals behind are two to four unpaired dermal bones termed the *pygal* plates or *postneurals*, the last of which, in shape and position, forms part of the marginal series. In addition to the posterior azygous marginal or pygal, there are eleven or twelve marginal plates on each side, except in *Staurotypus* and *Cinosternum*, which have but ten. The marginals and pygals are entirely dermal ossifications, and are usually absent in the *Trionychoidea*.

There are normally eight pairs of costal plates, but some fossil marine forms have nine or ten. The first costal is usually the broadest, the last

the smallest; in a few forms these plates are of unequal width, alternately widening proximally and narrowing distally. The distal extremity of the rib persists as a free point fitting into a corresponding socket of the marginal plate. In some forms there are persistent fontanelles or vacuities between the costal and marginal plates, and also in the plastron.

The *plastron* (Fig. 406, *C*) arises exclusively from dermal ossification, and is entirely independent of the pectoral arch, with which it has sometimes been homologised. It consists usually of nine bones, a median anterior *entoplastron*, and on each side following this in the order named, an *epiplastron*, a *hyoplastron*, a *hypoplastron*, and a *xiphiplastron*. An entoplastron is wanting among the *Cinosternidae*; and in *Baëna* and the *Pelomedusidae* the usual number



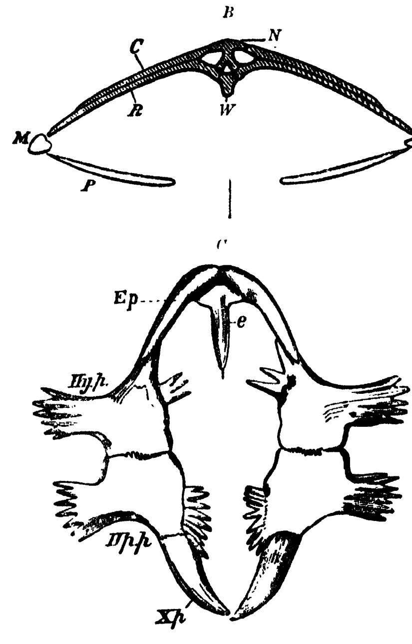


FIG. 406.

Chelone midas Latr. Recent; Atlantic Ocean. *A*, Dorsal aspect of carapace. *B*, Section of shell. *C*, Ventral aspect of plastron. C^1—C^8, costal plates; *e*, entoplastron; *Ep*, epiplastron; *Hyp*, hyoplastron; *Hpp*, hypoplastron; *M*, marginals; *N*, expanded neural spine; *Nu*, nuchal; *P*, plastron; *Py*, first pygal; *R*, ribs; *W*, vertebral centrum; *Xp*, xiphiplastron; 1—8, neural plates, followed by two pygals.

of nine bones is increased to eleven, the additional elements being the *mesoplastra*, situated between the hyo- and hypo-plastra. Until late in life in the *Chelydridae*, and throughout life in the *Cheloniidae*, the paired abdominal bones are separated by wide fontanelles (Fig. 406, *C*), while in all other Recent Cryptodires the plastron forms in the adult a solid shell, which may be divided into two or three portions by the presence of one or two transverse ligamentous hinges, as in *Cistudo*, *Cinosternum*, *Ptychogaster*, etc.

In the adult of most genera the hyo- and hypo-plastra are united with the marginal plates by suture. The part between the body of the plastron and the marginals is called the bridge; it is particularly short or absent in those *Testudinidae* in which the plastron is movable, and long and narrow in those forms (*Chelydridae*) in which the plastron is particularly small, the whole shield being cruciform. In such *Testudinidae* as have the plastron suturally united with the carapace, the hyo- and hypo-plastra send up

processes, respectively termed the axillary and inguinal buttress, which anchylose either with the inner surface of the marginals or with the costals; these buttresses are least developed in the land tortoises and most of the Cryptodires frequenting deep water, in which genera they form very large septa, nearly reaching the vertebral region and forming two lateral chambers occupied by the lungs (Boulenger).

The cervical region is extremely flexible, and comprises eight vertebrae, the first of which is biconcave, and the last biconvex. Except in certain primitive Triassic genera, there are no cervical ribs, and only rare traces of transverse processes. The ten rib-bearing dorsal vertebrae are immovably united with one another and with the carapace, following which are two (rarely three or more) flat-ended sacral vertebrae. The sacral ribs are, as on the last dorsal vertebra, suturally united with both centrum and neural arch; the first is the most developed, and considerably expanded distally. The caudal vertebrae are from sixteen to thirty-five, the more usual number being from twenty to twenty-five. The centra are in most cases procoelous, but sometimes opisthocoelous. Transverse processes or costoids are present on most of the vertebrae, and connected with the centrum and the arch. Neural spines are not developed, and chevron bones are usually absent or vestigial.

The bones of the *skull* (Fig. 407) form a broad, often very convex roof, which is usually prolonged behind in a strongly developed supraoccipital crest. The orbits are large and placed laterally in advance of the middle of the skull; the deeper the skull, the larger the orbits. The latter are completely encircled by four or five bones—the maxilla, prefrontal, sometimes the frontal, the postfrontal, and the jugal. The external nostril is terminal and almost always single, bounded by the premaxillae, maxillae, and prefrontals or nasals. The parietals are of large size and distinct, being connected with the palate (except in the *Dermochelyidae*) by lateral descending processes. An independent lachrymal bone is rarely present (*Triassochelys, Chisternon, Kallokibotium*), and separate nasals occur only among the *Amphichelydia*, most *Pleurodira*, and some *Cryptodira*. The anterior margin of the snout is formed by the small, usually distinct premaxillae.

The postfrontals are large in most Cryptodires, forming a postorbital arch; in the marine turtles the postfrontal unites in a long suture with the parietal, the whole or greater part of the temporal region being roofed over by bone. The temporal roof attains its greatest development in the *Cheloniidae* and *Dermochelyidae*, where three cranial arches are present—the postfronto-squamosal, the jugo-quadratojugal, and the parieto-squamosal. In all other Cryptodires the parietal is widely separated from the squamosal, and as a rule the squamosal is separated from the postfrontal. In a few genera there is no bony temporal arch, and the quadrato-jugal is rudimentary or absent. The jugal, when present, takes part with the maxilla in the lower border of the orbit, being excluded from it only in the genus *Platysternum*. The proötic and opisthotic are both stout bones, situated in their usual positions. The exoccipital sometimes fuses with the supraoccipital, which is produced beyond a line drawn between the posterior extremities of the squamosal. The foramen magnum is deeper than broad, and bounded by the supraoccipital and the exoccipitals, and occasionally also by the basioccipital. The exoccipitals and basioccipital usually form a tripartite occipital condyle.

The squamosal joins both the proötic and opisthotic, and is buttressed by the quadrate, which penetrates the otic region by means of a superiorly or inwardly directed process, and is suturally connected with the quadrato-jugal. The quadrate, which is curved round the otic notch behind, sometimes joins both the basisphenoid and basioccipital, but in all Cryptodires it is separated from the basisphenoid by the pterygoids, which form a suture with the basioccipital, or very nearly reach the latter bone, and are in contact with the maxillae (except in the *Cheloniidae*). In none of the Pleurodires do the

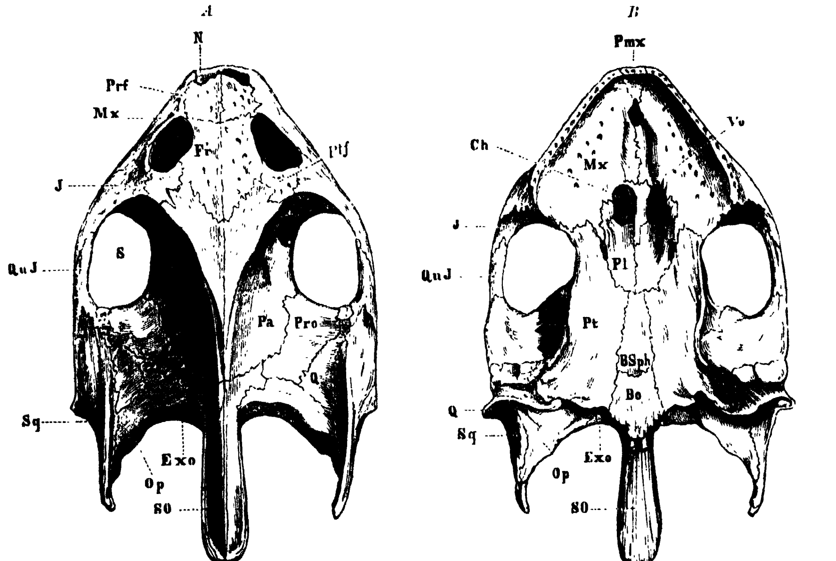


Fig. 407.

Trionyx gangeticus Cuvier. Recent; India. Superior (*A*) and palatal (*B*) aspects of skull, reduced. *A*, orbit; *Bo*, basioccipital; *BSph*, basisphenoid; *Ch*, internal nares; *Exo*, exoccipital; *Fr*, frontal; *J*, jugal. *Mx*, maxilla; *N*, external nostril; *Op*, opisthotic; *Pa*, parietal; *Pl*, palatine; *Pmx*, premaxilla; *Prf*, prefrontal + nasal; *Pro*, proötic; *Pt*, pterygoid; *Ptf*, postfrontal; *Q*, quadrate; *QuJ*, quadrato-jugal; *S*, supratemporal fossa; *So*, supraoccipital; *Sq*, squamosal; *Vo*, vomer (after Hoffmann).

pterygoids extend posteriorly beyond the quadrate. The vomer is single and separates the internal nares. The stapes (*columella auris*) is ossified.

The mandibular elements, which are six in number, are so intimately united in the adult as to appear like a single piece. A symphysial suture is present in the *Chelydridae*, however, at least in young individuals. In the Triassic genus *Triassochelys* small teeth occur on the palate, and apparently rudiments of a single row of teeth are found on the marginal bones of the jaws. In all other Chelonians teeth are absent, but the edges of the jaws are covered with sharp, horny sheaths like the beak of a bird.

The pectoral and pelvic arches (Fig. 408) are remarkable as being enclosed within the shell, but since they are both external to the ribs in the embryo, their apparently abnormal position is seen to be a secondary modification. Of the three branches which constitute the pectoral arch, namely, the scapula, acromion (or "precoracoid"), and coracoid, the latter is longest in the *Cheloniidae*, the former in all other Cryptodires. The coracoids are long, distally expanded bones, directed backwards and inwards, but not

meeting in the median line. The scapula is slender, rod-like, and upwardly directed. Its distal extremity is attached by ligament or cartilage to the anterior costal bone, and its proximal end bears an elongated acromial process (precoracoid of many authors, proscapula of Baur, clavicle of Cuvier and Owen). The latter is directed forwards and downwards, and its expanded distal end is attached by ligament to the entoplastron. Clavicles and cleithra are also present in the primitive genus *Triassochelys*. The humerus exhibits a large spherical head and a more or less strongly curved shaft, often with ectepicondylar foramen or notch at its distal end. The radius and ulna are of about equal length, except in the *Cheloniidae*, where the former is much longer and situated below the ulna. The proximal carpals are commonly four, and the distal five in number; numerous variations, however, are exhibited by the bones of the manus among the different families and genera. Five digits are always present, but sometimes not more than three are clawed. The first digit usually has two, the others have three phalanges; but in the *Testudinidae* this number is often reduced, while in the *Trionychoidea* the fourth digit bears one or two additional joints.

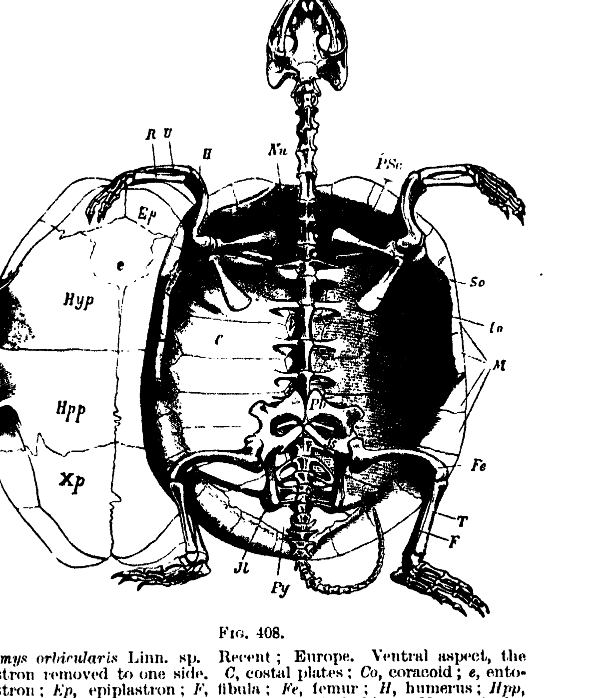


FIG. 408.

Emys orbicularis Linn. sp. Recent; Europe. Ventral aspect, the plastron removed to one side. *C*, costal plates; *Co*, coracoid; *e*, entoplastron; *Ep*, epiplastron; *F*, fibula; *Fe*, femur; *H*, humerus; *Hpp*, hypoplastron; *Hyp*, hyoplastron; *Jl*, ilium; *Js*, ischium; *M*, marginals; *Nu*, nuchal; *Pb*, pubis; *Psc*, acromion; *Py*, pygal; *R*, radius; *Sc*, scapula; *T*, tibia; *U*, ulna; *Xp*, xiphiplastron.

In the pelvic arch the long ilium is loosely attached to the sacrum and eighth costal plate in the *Cryptodira*, to the sacral ribs in the *Trionychoidea*; but in all existing *Pleurodira* the pelvis is solidly united with the carapace and plastron, and bears no trace of sacral attachment (Fig. 417). The pubis and ischium of Cryptodires form a ventral symphysis, and their symphysial branches are either widely separated from each other, or in contact and limiting a pair of ischio-pubic fenestrae (*Testudinidae*). The pubis sends off a more or less developed process, directed forwards and outwards, which may be subcylindrical, rod-like, or flat and expanded distally; a lateral process is also present, but usually less developed than that of the pubis, on the ischium of all Cryptodires except the *Cheloniidae* (Boulenger). The femur is a curved cylindrical bone, and the tibia and fibula are subequal in length. An astragalus (formed of the tibiale + intermedium) which is in contact with both tibia and fibula, and a small

outer calcaneum (fibulare) constitute the proximal tarsals; or among the *Emydidae* these may coalesce in a single piece. A centrale is distinct in the *Chelydridae* and most Pleurodires; and except in the *Cheloniidae*, which have four, the distal row of tarsals contains five bones.

Habitat and Geological History.—Many of the *Chelonia* are terrestrial in habit, a greater number are aquatic, and a few are exclusively marine. The Recent species are mostly limited to the tropics or warm temperate zones. They lay eggs on the ground or on the sandy shores of the sea, lakes, or rivers. Many

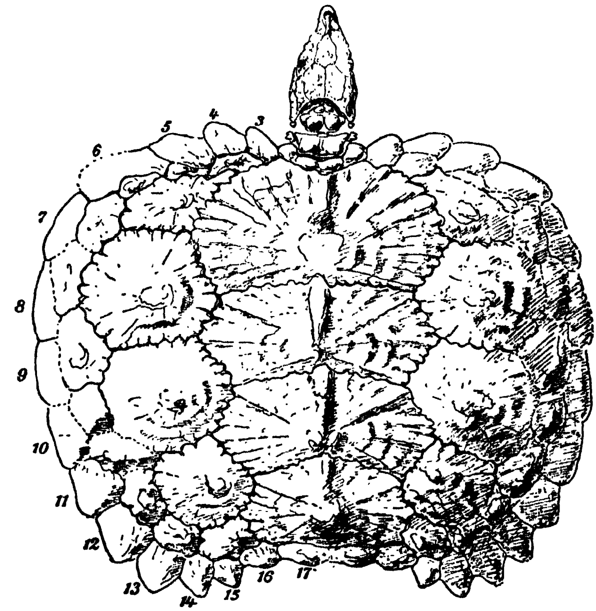


Fig. 409.
Triassochelys dux Jaekel. Carapace with skull. Upper Keuper; Halberstadt, N. Germany. 3-17, marginals. 1/8 nat. size (after Jaekel).

of them feed chiefly on plants, but others also on fishes, molluscs, and crustaceans. The earliest known fossil remains are from the Upper Keuper of Germany, and are fortunately well preserved. None have been discovered in Lower Jurassic rocks, but from the Upper Jurassic of Switzerland, Northern France, Germany, England, and the United States many forms are known, all closely similar to existing genera. Numerous Chelonian remains occur in the Cretaceous and Tertiary, but complete skeletons in association with the shell are extremely rare. The only noteworthy marks of evolution in the Order since early Cretaceous time are degeneration of the carapace and plastron in certain types, and elongation of the phalanges in specially aquatic forms.

Sub-Order 1. AMPHICHELYDIA.[1]

Roof of temporal region of skull complete; nasal bones separate. Cervical vertebrae short, with transverse processes, sometimes also ribs; head not retractile in

[1] *Hay, O. P.*, The Group of Fossil Turtles known as the Amphichelydia. Bull. Amer. Mus. Nat. Hist., vol. xxi., p. 137, 1905.

shell. Shell complete, with marginals and mesoplastra; inframarginal and intergular shields present. Pelvis in contact with both carapace and plastron, but usually not anchylosed with the latter.

This group was established by Lydekker to include a number of generalised Mesozoic forms having a shell constructed on the plan of that in Cryptodires and Pleurodires, in which mesoplastral bones and an intergular shield are developed. The pubes and ischia are more or less closely attached to the plastron; and, according to Nopcsa, they sometimes approach the Cryptodiran shape (*Triassochelyidae*, *Pleurosternidae*, *Baenidae*), sometimes the Pleurodiran (*Proterochersidae*, *Kallokibotiidae*).

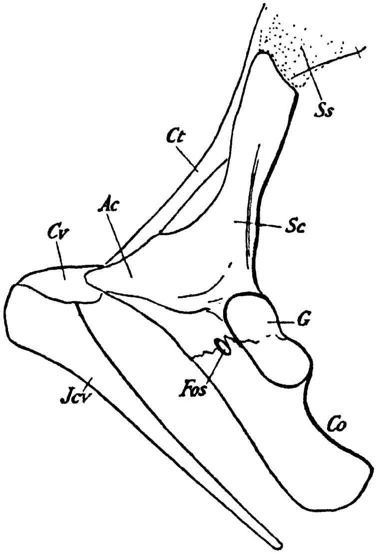


FIG. 410.

Triassochelys dux Jaekel. Pectoral arch. Upper Keuper; Halberstadt, N. Germany. *Ac*, acromion; *Co*, coracoid; *Ct*, cleithrum; *Cv*, clavicle; *Fos*, supracoracoid foramen; *G*, glenoid fossa; *Jcv*, interclavicle; *Sc*, scapula; *Ss*, suprascapular cartilage. Much reduced (after Jaekel).

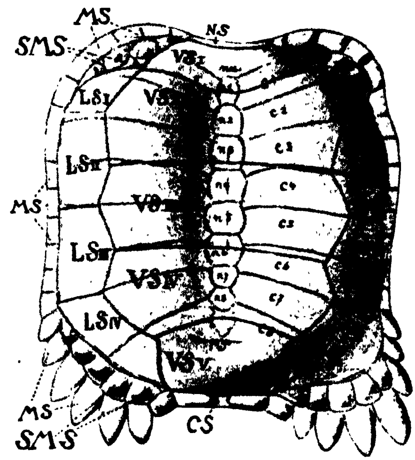


FIG. 411.

Proganochelys quenstedti Baur. Carapace. Keuper; Aixheim, Würtemberg. Epidermal shields lettered *CS* (caudal), *LS* I-IV (costal), *MS* (marginal), *NS* (nuchal), *SMS* (supramarginal), and *VS* I-V (vertebral). Bony plates lettered c^{1-8} (costals), n^{1-8} (neurals), *nu* (nuchal), and *py* (pygal). About $^1/_{10}$ nat. size (after E. Fraas).

Family 1. **Triassochelyidae.**[1]

Land tortoises with deep body. Teeth at least on the palate. Quadrate bone straight. Cervical vertebrae amphicoelous, and ribs present. Acromial process of scapula short; cleithrum present. Pelvis not fused with shell. Supplementary epidermal shields between the costals and marginals. Upper Triassic.

Triassochelys Jaekel (*Stegochelys* Jaekel *nec* Lydekker) (Figs. 409, 410). Skull with simple basioccipital condyle. A cluster of small, blunt conical teeth on the vomer, parasphenoid, and pterygoids; rudiments of a single row of teeth in small pits a little within the sharp margin of the upper and

[1] *Fraas, E.*, *Proganochelys quenstedtii* Baur (*Psammochelys keuperina* Qu.). Jahresb. Ver. f. vaterl. Naturk. Württ., 1899, p. 401.—*Jaekel, O.*, Wirbeltierfunde aus dem Keuper von Halberstadt. II. Testudinata. Palaeont. Zeitschr., vol. ii., p. 88, 1915.

lower jaws. Eight cervical vertebrae with double-headed ribs; conical dermal tubercles on the neck. Sacrum of two vertebrae. A complete row of epidermal shields between the costals and marginals. *T. dux* Jaekel, known by the greater part of a skeleton and fragments from the Upper Keuper of Halberstadt, N. Germany, with skull about 20 cm., and carapace about 65 cm. in length.

Proganochelys Baur (*Psammochelys* Quenstedt) (Fig. 411). Shell as in *Triassochelys*, but row of supplementary epidermal shields between costals and marginals restricted to short anterior and posterior portion. *P. quenstedti* Baur, known only by the shell 65 cm. in length, from the Keuper of Würtemberg.

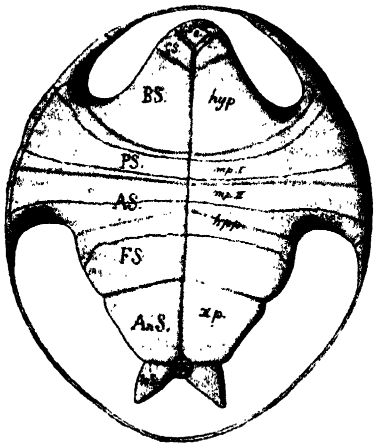


FIG. 412.
Proterochersis robusta E. Fraas. Plastron. Keuper; Rudersberg, Würtemberg. Epidermal shields lettered *AnS* (anal), *AS* (abdominal), *BS* (brachial), *CS* (intercaudal), *FS* (femoral), *GS* (gular), *IcS* (caudal), *IGS* (intergular). About 1/5 nat. size (after E. Fraas).

Family 2. **Proterochersidae.**[1]

Land tortoises with deep body. Pelvis fused with shell, rather Pleurodiran. Vertebral shields broad; supplementary epidermal shields between the costals and marginals. Upper Triassic.

Proterochersis E. Fraas (Fig. 412). With two pairs of mesoplastra. Sacrum of four vertebrae. *P. robusta* E. Fraas, known only by imperfect shell about 30 cm. in length and very deep, from the Keuper of Würtemberg.

Chelytherium H. von Meyer. Keuper; Würtemberg.

? *Chelyzoon* F. von Huene. Vertebrae from Muschelkalk.

? *Saurodesmus* Seeley. Femur from Rhaetic; Nairn, Scotland.

Family 3. **Pleurosternidae.**[2]

Water tortoises with depressed body. Cervical vertebrae amphicoelous, without ribs. Acromial process of scapula long; no cleithrum. Carapace united with plastron by narrow buttresses. Upper Jurassic and Cretaceous.

Pleurosternum Owen (*Megasternon* Gray). Carapace much depressed, rounded posteriorly, without vacuities, and firmly united with the plastron, which is also continuous. Surface of shell very finely pitted and deeply impressed with the suture-lines of the epidermal shields. Neural bones moderately elongated, hexagonal, with their anterolateral surfaces short. Mesoplastrals well developed, meeting in the middle line; entoplastral relatively large; xiphiplastrals deeply notched. No nuchal shield; intergular shield not divided; inframarginals present. Pectoral arch resembling that

[1] *Fraas, E.*, *Proterochersis*, eine pleurodire Schildkröte aus dem Keuper. Jahresh. Ver. f. vaterl. Naturk. Württ., 1913, p. 13.—*Huene, F. von*, Einige Schildkrötenreste aus der obersten Trias Württembergs. Centralbl. f. Min., etc., 1926, Abt. B., p. 509.

[2] *Haughton, S. H.*, Reptilian Remains from the Dinosaur Beds of Nyasaland. Trans. Roy. Soc. S. Africa, vol. xvi., p. 68, 1928.—*Nopcsa, F.*, *Helochelydra*. Geologica Hungarica, Ser. Palaeont., vol. i., p. 44, 1928.—*Watson, D. M. S.*, *Glyptops ruetimeyeri* (Lyd.), a Chelonian from the Purbeck of Swanage. Geol. Mag. [5], vol. vii., pp. 311, 381, 1910.

of the existing *Chelys*. *P. bullocki* Owen. Purbeck Beds; England. Also Wealden; N. Germany.

Platychelys Wagner (*Helemys* Rütimeyer) (Fig. 413). Ridges or pro-

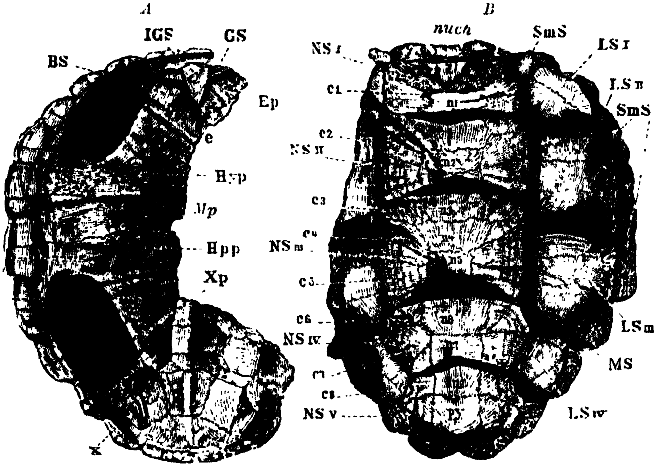


FIG. 413.

Platychelys oberndorferi Wagner. *A*, Plastron. *B*, Carapace. Upper Jurassic; Kelheim, Bavaria. *BS*, brachial shield; *Ep*, epiplastron; *GS*, gular shield; *Hpp*, hypoplastron; *Hyp*, hyoplastron; *IGS*, intergular shield; *LS* I-IV, lateral shields; *Mp*, mesoplastron; *MS*, marginal shields; *NS* I-V, neural or vertebral shields; *SmS*, supramarginal shield; *Xp*, xiphiplastron; c^{1-8}, costal plates; *e*, entoplastron; n^{1-8}, neural plates; *nuch*, nuchal; *py*, pygal; *x*, pit for attachment of ilium. 1/4 nat. size.

minences on the neurals and costals. Neurals short and of irregular contour, the width usually much exceeding the length. Mesoplastrals not meeting in the middle line. Vertebral shields much wider than long; nuchal shield present; intergular undivided. Upper Jurassic; Bavaria, France, and England.

Platycheloides Haughton. Lower Cretaceous; Nyasaland.

Glyptops Marsh. Anterior edge of carapace emarginate. Nuchal shield present. Mesoplastron complete, much resembling that of *Pleurosternum*. Hinder lobe of plastron deeply notched. Upper Jurassic to Upper Cretaceous; N. America. Purbeck Beds; England.

Tretosternum Owen. Shell tuberculated, impressed with the suture-lines of the epidermal shields. Nuchal deeply emarginate. Purbeck and Wealden; England. *Stegochelys* Lydekker. Portlandian.

Helochelys H. von Meyer. Cenomanian; Kelheim, Bavaria.

Helochelydra Nopcsa. Wealden; Isle of Wight.

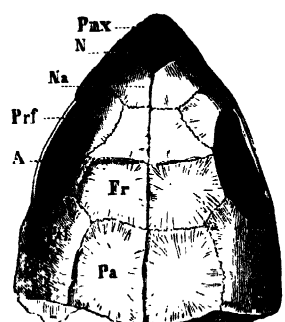


FIG. 414.

Rhinochelys cantabrigiensis Lydekker. Skull, upper aspect. Cambridge Greensand. *A*, orbit; *Fr*, frontal; *N*, nostril; *Na*, nasal; *Pa*, parietal; *Pmx*, premaxilla; *Prf*, prefrontal; *Ptf*, postfrontal. Nat. size (after Lydekker).

Trachydermochelys, *Rhinochelys* Seeley (Fig. 414). Cambridge Greensand and Upper Greensand; England. The type specimen of *T. rutteri* Andrews has two mesoplastra on one side, one on the other.

? *Protochelys* Lydekker. Epidermal shields from the Stonesfield Slate, Oxfordshire.

Family 4. **Baenidae.**[1]

Water tortoises with depressed body. Skull short. Cervical vertebrae usually with only one end concave, without ribs. Acromial process of scapula long; no cleithrum. Carapace united with plastron by wide strong buttresses. Upper Jurassic, Cretaceous, and Eocene.

Baëna Leidy. Intergular shield divided, and xiphiplastral with depressions which appear to have received the pubis and ischium. Mesoplastrals meeting in the middle line, but with the median ends much narrower than the outer ends. Upper Cretaceous and Eocene; N. America.

Probaena Hay. Fontanelle between inner ends of mesoplastra. Upper Jurassic (Morrison Formation); Colorado.

Naomichelys Hay. Plastron tuberculated. Upper Jurassic; Montana.

Eubaena, Thescelus, Charitemys Hay. ?*Polythorax* Cope. Upper Cretaceous; N. America.

Boremys, Neurankylus Lambe. In *Boremys pulchra* Lambe there are three pairs of large supramarginal shields in line with the second, third, and fourth vertebral shields. Upper Cretaceous; Alberta, Canada; Wyoming and New Mexico, U.S.A.

Chisternon Leidy. Middle Eocene (Bridger Beds); Wyoming.

Family 5. **Kallokibotiidae.**[2]

Much resembling Baenidae, *but narial opening divided by the premaxillae, cervical vertebrae amphicoelous, acromial process of scapula short and stout, and pelvis more Pleurodiran.* Upper Cretaceous.

Kallokibotium Nopcsa. Pterygoids with longitudinal ridges. Short cervical vertebrae amphicoelous; caudal vertebrae depressed. Pelvis fused with plastron in adult. *K. bajazidi* Nopcsa, with skull about 40 cm. in length, from Upper Cretaceous (Danian), Transylvania.

Sub-Order 2. PLEURODIRA.

Roof of temporal region of skull sometimes complete, but usually emarginated from below. Outer border of tympanic cavity completely encircled by the quadrate; pterygoids very broad throughout, forming wing-like lateral expansions, and not separating the quadrates and basisphenoid; nasals free or united with prefrontals; the latter without descending processes. Neck bending laterally under shell, but cervical vertebrae usually with transverse processes. Shell usually complete and covered with epidermal shields; epiplastra in contact with hyoplastra; mesoplastrals present in some forms, and an intergular in all cases where epidermal shields occur. Pelvis anchylosed to carapace and plastron. Digits with not more than three phalanges.

In this group, as indicated by the name, the neck bends laterally, and the pelvis is anchylosed to the carapace and plastron. Existing Pleurodires are almost restricted to the southern hemisphere, and distributed in South

[1] *Lambe, L. M., Boremys*, a new Chelonian Genus from the Cretaceous of Alberta. Ottawa Nat., vol. xix., p. 232, 1906.

[2] *Nopcsa, F., Kallokibotium*, a primitive Amphichelydian Tortoise from the Uppermost Cretaceous of Hungary. Palaeont. Hungarica, vol. i., p. 1, 1923.

America, Southern India, Africa, Madagascar, New Guinea, and Australia. The fossil *Plesiochelyidae*, *Thalassemydidae*, and *Miolaniidae* are referred by Nopcsa to the *Amphichelydia*.

Family 1. **Plesiochelyidae.**[1]

Skull with temporal region completely roofed. Shell usually thick, without mesoplastra, and with either a reduced or the full number of neurals and suprapygals; only the pubis uniting with the xiphiplastral; entoplastral small; inframarginal shields at least usually present. Sometimes a plastral vacuity. Phalangeals reduced. Upper Jurassic and Wealden.

Plesiochelys Rütimeyer (*Stylemys* Maack *nec* Leidy) (Fig. 415). Shell attaining a length of 0·5 m., circular or cordiform, relatively thick, consider-

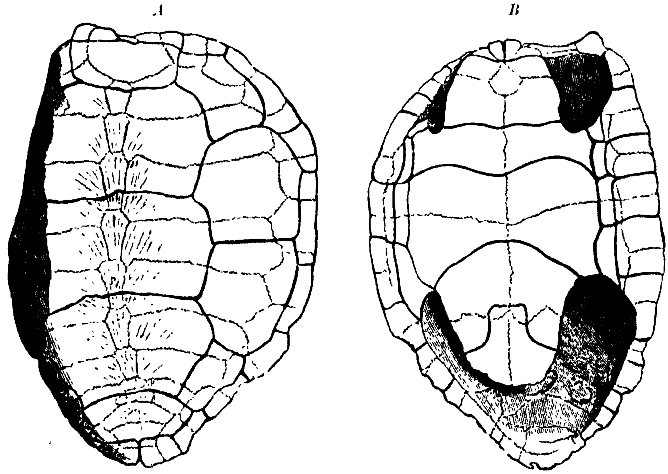


FIG. 415.

Plesiochelys solodurensis Rütimeyer. *A*, Carapace. *B*, Plastron. Upper Jurassic (Kimmeridgian); Solothurn, Switzerland. $^1/_8$ nat. size (after Rutimeyer).

ably vaulted in the adult, and with or without a persistent plastral vacuity. Nuchal more or less emarginate; neurals generally long and narrow, and connected with the first of the three suprapygals. Plastral bridge long; sulcus between abdominal and femoral shields ascending towards the hypoplastral suture, and terminating in the middle of the inguinal notch. Upper Jurassic; Germany, Switzerland, and France.

Hydropelta, *Parachelys* v. Meyer. Upper Jurassic; Europe. *Tholemys* Andrews. Kimmeridge Clay; Swindon. *Hylaeochelys* Lydekker. Upper Jurassic and Wealden; Europe. *Brodiechelys* Nopcsa. Wealden; Isle of Wight.

[1] *Andrews, C. W.*, New Chelonian from the Kimmeridge Clay of Swindon [*Tholemys passmorei*]. Ann. Mag. Nat. Hist. [9], vol. vii., p. 145, 1921.—*Hooley, R. W.*, Tortoise [*Plesiochelys*] from the Wealden of the Isle of Wight. Geol. Mag. [4], vol. vii., p. 263, 1900.—*Nopcsa, F.*, *Hylaeochelys*. Geologica Hungarica, Ser. Palaeont., vol. i., p. 48, 1928.—*Oertel, W.*, Schildkrötenfauna des nordwestdeutschen oberen Jura. Palaeont. Zeitschr., vol. vi., p. 43, 1924.

Family 2. **Thalassemydidae.**[1] (*Acichelyidae* Lydekker.)

Temporal fossae of skull partially roofed. Shell cordiform, more or less incompletely ossified, the median fontanelle in plastron persisting for a long period or throughout life. Nuchal without costiform process. Plastron connected with carapace by axillary and inguinal buttresses. Humerus with imperfectly developed head and nearly straight shaft. Phalanges with articular condyles, all the terminal phalanges clawed. Upper Jurassic and Cretaceous.

This family includes late Mesozoic genera which combine the characters of both marine and marsh turtles, but appear to have been mainly marine. The very incomplete ossification of the carapace and the persistent fontanelle of the plastron are as in sea-turtles, while the form of the plastral elements and the outwardly bent extremities of the hyo- and hypoplastrals are suggestive of marsh forms. The five functional toes with articulating phalanges were all clawed and probably webbed in life, being adapted both for progression on land and for swimming.

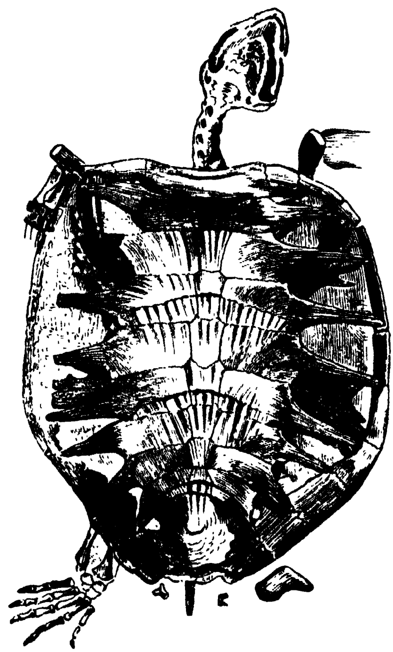


Fig. 416.
Eurysternum wagleri v. Meyer. Upper Jurassic; Zandt, near Eichstädt, Bavaria. 1/3 nat. size.

Thalassemys Rütimeyer (*Enaliochelys* Seeley). Carapace moderately thick, flattened, with well-ossified costals, the posterior neurals not forming a tectiform ridge. Vertebral shields narrow. No mesoplastron. Very large persistent vacuities in the plastron. Upper Jurassic; Switzerland, Würtemberg, and England.

Eurysternum Wagler (*Achelonia*, *Acichelys*, *Aplax*, *Palaeomedusa* v. Meyer; *Euryaspis* Wagner) (Fig. 416). Carapace flattened, distinctly emarginate anteriorly, with the costals well ossified and posterior neurals not forming a tectiform ridge. Vertebral shields very wide, marginals long and narrow. No mesoplastron. Plastron with large persistent vacuities. Upper Jurassic (Lithographic Stone); Bavaria and Cerin, Ain, France.

Tropidemys Rütimeyer; *Pelobatochelys* Seeley. Upper Jurassic and Wealden; Europe.

Chelonides Maack. Upper Jurassic; N. Germany.

Idiochelys H. von Meyer (*Chelonemys* Jourdan). Neurals partly reduced. No mesoplastron. Plastron with only lateral vacuities. Upper Jurassic (Lithographic Stone); Bavaria and Cerin, Ain, France.

Desmemys Wegner. Nasal bones separate. Mesoplastron present. Wealden; Westphalia.

[1] *Fraas, E.*, *Thalassemys marina*. Jahresh. Ver. f. vaterl. Naturkunde Württ., 1903, p. 72.—*Stache, G.*, *Sontiochelys*, etc. Verhandl. k. k. geol. Reichsanst. Wien, 1905, p. 285.—*Wegner, T.*, *Desmemys bertelsmanni* n.g. n.sp. Ein Beitrag zur Kenntnis der *Thalassemydidae* Rütimeyer. Palaeontogr., vol. lviii., p. 105, 1911.

Desmatochelys Williston (? *Atlantochelys* Agassiz; ? *Neptunochelys* Wieland). Large separate nasal bones. Plastron loosely joined to carapace. *D. lowi* Williston. Upper Cretaceous; Nebraska, U.S.A.

? *Pygmaeochelys* Laube. Turonian; Bohemia.

? *Sontiochelys* Stache. No neurals. Cenomanian; Görz.

Family 3. **Miolaniidae.**[1]

Shell known only by fragments. Skull with temporal fossae completely roofed, and with horn-like bony protuberances; no distinct nasals; vomer dividing palatines. Caudal vertebrae opisthocoelous, with chevrons; tail long and encased in a nodose bony sheath. Pleistocene (? also Cretaceous).

Miolania Owen (*Ceratochelys* Huxley; *Niolamia* Ameghino). Cranium with three pairs of peripheral prominences in the fronto-parietal region, the head measuring in one species 0·6 m. in width to the tip of the "horns." Probably herbivorous and terrestrial. *M. platyceps* Owen; *M. oweni* A. S. Woodw. Pleistocene; Lord Howe Island and Queensland. *M. mackayi* Anderson. Pleistocene; Walpole Island, 100 miles S.E. of New Caledonia. *M.* (*Niolamia*) *argentina* Ameghino, with occipital crest relatively large, postero-lateral horns triangular in section, a simple blunt ridge round the palate, and no internasal septum. Supposed Cretaceous; Chubut, Argentina.

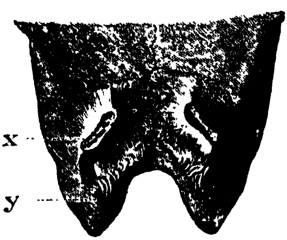


Fig. 417.

Podocnemis expansa Wagler. Recent; Brazil. Visceral aspect of posterior end of plastron, showing places for attachment of pubes and ischia, *x*, *y* (after Rutimeyer).

Family 4. **Pelomedusidae.**[2]

Temporal region of skull partially roofed. No free nasals; prefrontals in contact. Palatine bones meeting in middle line. Second cervical vertebra biconvex. Mesoplastra present. Tertiary and Recent.

This family includes the Recent genera *Pelomedusa* Wagler, *Sternothaerus* Bell, and *Podocnemis* Wagler (Fig. 417). The two first are found fossil in the Lower Miocene and Pliocene of Egypt; the third dates back to the Lower Eocene in England, the Middle Eocene in Peru, the Middle and Upper Eocene in Egypt, and the Lower Miocene in British East Africa.

Bantuchelys Dollo. As *Podocnemis*, but carapace with rugose ornament, and the Y-shaped groove absent on the first costal plate. *B. congolensis* Dollo. Paleocene (Montian); Landana, Congo Free State.

Stereogenys Andrews. With very broad crushing mandibular symphysis. Upper Eocene; Egypt.

Family 5. **Bothremydidae.**[2]

As Pelomedusidae *but with enlarged vomer and crushing surface of jaws ending in a deep pit behind.* Upper Cretaceous.

[1] *Anderson, C.*, The Extinct Chelonian *Meiolania*, with a Record of a new Occurrence. Rec. Australian Mus., vol. xiv., p. 223, 1925; also *loc. cit.*, vol. xvii., p. 309, 1930, and Australian Mus. Mag., 1926, p. 360.—*Woodward, A. S.*, Proc. Zool. Soc., 1901, p. 170.

[2] *Dollo, L.*, *Bantuchelys*, Genre nouveau de tortues découvert dans le Paléocène du Congo. Bull. Acad. Roy. Belg., Classe Sci., 1924, p. 613.—*Nopcsa, F.*, Tortues du Danien du Midi de la France. Bull. Soc. Géol. France [5], vol. i., p. 223, 1931.—*Schmidt, K. P.*, Fossil Turtle from Peru. Field Mus. Nat. Hist., Chicago, publ. 299, 1931.

Bothremys Leidy. Vomer not separating palatines. Known only by skull from New Jersey, U.S.A.

Taphrosphys Cope (*Prochonias* Cope). Known only by shell, which is more or less sculptured. Mesoplastra small. New Jersey.

Amblypeza Hay. New Jersey.

Naiadochelys Hay. Shell not sculptured. New Mexico, U.S.A.; Patagonia.

Elochelys Nopcsa. Danian; S. France.

Family 6. **Chelyidae.**

Temporal region of skull usually partially roofed; frontal unpaired; nasals free; premaxillae distinct. Palatine bones separated by vomer. No mesoplastra; no inframarginal shields. Wealden, Tertiary and Recent.

Chelys Duméril; *Hydromedusa* Wagler. Recent.

Chelodina Fitzinger. Neural bones absent, and the external surface more or less vermiculated. Pleistocene and Recent.

Rhinemys Wagler (*Phrynops* Wagler; *Hydraspis* Bell). Eocene; India. Recent; South America.

Emydura Bonap. Pleistocene and Recent; Australia. *Platemys* Wagler; *Elseya* Gray. Recent.

Chitracephalus Dollo. Cranium much elongated and depressed, with an extremely short facial region. Cervical vertebrae without transverse processes. Costals narrowed at their outer ends, with vacuities within the well-developed border of the marginals. Plastral elements similar to those of *Chelone*. Digits clawed, not greatly elongated. *C. dumoni* Dollo. Wealden; Belgium.

Sub-Order 3. CRYPTODIRA.

Roof of temporal region of skull sometimes complete, but usually emarginated from behind. Stapes in a groove which usually remains open behind. Pterygoids extending backwards between the quadrates and basisphenoid. Rarely free nasals; descending process of the prefrontals connected with the vomer. Neck bending by a sigmoid curve in a vertical plane. Cervical vertebrae without or with mere indications of transverse processes. Pelvis not anchylosed with carapace or plastron. Digits with not more than three phalanges. Epiplastra in contact with hyoplastra; entoplastron oval, rhomboidal or T*-shaped, or wanting; no mesoplastra. A complete series of marginal bones, connected with the ribs.*

This Sub-order comprises the majority of existing and fossil Chelonians. It is distinguished from the *Pleurodira* by having the head retracted by curvature of the neck in a vertical plane, and the pelvis unconnected with the plastron. The head is completely retractile within the shell in the land and freshwater forms.

Family 1. **Chelydridae.**

Roof of temporal region of skull incomplete; no parieto-squamosal arch. Frontals excluded from orbit; maxilla separated from the quadrato-jugal; squamosal in connection with postorbito-frontal. Epidermal shields absent in some cases; number of neurals complete; posterior costals meeting in the median line. Shell usually not fully ossified until late in life. Plastron frequently small, cruciform, articulating with the carapace by gomphosis. Nuchal emarginate, with long

costiform processes underlying the anterior marginals. Eleven marginals on each side; a series of inframarginal shields. Limbs not modified into paddles; digits moderately elongate, webbed; claws four or five. Dermal plates on tail. Eocene to Recent.

Gafsachelys de Stefano. Eocene; Gafsa, Tunis.

Acherontemys Hay. Marginals more closely articulated with the costals than in the existing *Chelydridae*. Vertebral shields very broad. *A. heckmani* Hay. Miocene; Roslyn, Washington State, U.S.A.

Chelydra Schweigger. Nuchal not very deeply emarginated; neural bones mostly hexagonal; supramarginal shields absent; posterior border of carapace serrated. Oligocene to Recent. *C. murchisoni* Bell. Upper Miocene; Oeningen, Baden. *C. decheni* H. v. Meyer. Upper Oligocene; Bonn, Germany. Recent and Pleistocene in North and Central America.

Macroclemmys Gray (*Macrochelys* Gray; *Gypochelys* Agassiz). Recent and Pleistocene in North America.

Devisia D. Ogilby. Recent; New Guinea.

Family 2. **Dermatemydidae.**[1]

Skull with temporal region emarginated behind; frontals not excluded from orbit; maxilla unconnected with quadrato-jugal, and squamosal separated from postorbito-frontal. Shell covered with epidermal shields; plastral shields separated from the marginals by a series of inframarginals. Plastron united with the carapace by suture or ligaments. Nuchal bone with costiform processes underlying the anterior marginals. Number of neurals incomplete; posterior costals not meeting in the median line. Pubic and ischiadic symphyses widely separated. Digits moderately elongate, claws four or five. No dermal plates on tail. Cretaceous to Recent.

This family exists in Central America, and there are some fossil forms, such as *Adocus*, *Agomphus* (*Amphiemys*), *Homorophus*, *Zygoramma* Cope, *Compsemys* Leidy, and *Basilemys* Hay, from the Upper Cretaceous of North America; *Sinochelys* Wiman, from the Lower Cretaceous of Shantung, China; *Peltochelys* Dollo, from the Wealden of Belgium; *Notomorpha* Cope and *Baptemys* Leidy, *Alamosemys*, *Hoplochelys*, and *Kallistira* Hay, from the Eocene of New Mexico; *Xenochelys* Hay, from the Oligocene of South Dakota; and *Trachyaspis* von Meyer, from the Tertiary of Europe and Africa. The family is intermediate in position between the *Chelydridae* and *Cinosternidae*, and in some respects suggestive of Pleurodires. *Adocus*, from the American Cretaceous, was made by Cope the type of an independent family, characterised by the abortion of the heads of the ribs.

Of the American **Cinosternidae**,[2] *Cinosternum* (*Kinosternon*) Spix occurs in the Pliocene of Arizona, but *Aromochelys*, *Goniochelys*, *Staurotypus*, and *Claudius* are unknown among fossils.

The **Platysternidae** with the solitary genus *Platysternum* Gray, found in

[1] *Lambe, L. M.*, Turtle from the Cretaceous Rocks of Alberta [*Adocus*]. Ottawa Nat., vol. xv., p. 63, 1901.—*Wieland, G. R.*, Structure of the Upper Cretaceous Turtles of New Jersey: *Adocus*, etc. Amer. Journ. Sci. [4], vol. xvii., p. 112, 1904.—*Agomphus*. *Loc. cit.*, vol. xx., p. 430, 1905.—*Riggs, E. S.*, *Basilemys sinuosus*. Field Columbian Mus., Chicago, Publ. 110, 1906.

[2] *Nopcsa, F.*, Case of Secondary Adaptation in a Tortoise. Ann. Mag. Nat. Hist. [9], vol. x., p. 155, 1922.

S. China, Burma, Siam, and the Philippines, seem to be represented by *Scutemys* Wiman in the Lower Cretaceous of Shantung, China.

Family 3. **Emydidae.**[1] Marsh Tortoises.

Skull with open temporal fossae; otic notch of quadrate open behind. Shell completely ossified in the adult, covered with epidermal shields. Carapace only moderately convex; nuchal bone without prominent costiform processes. Plastron sometimes hinged, with long sternal bridge and large sternal chambers, the marginals of bridge without median processes interlocking with the rib-ends. No inframarginal shields. Feet nearly always webbed; second and third digits usually with more than two phalanges; claws four or five. Eocene to Recent.

The *Emydidae* or Marsh Tortoises are very closely related to the *Testudinidae* or Land Tortoises, and are sometimes included with them in the same family. The shell, however, in the Emyds is less convex, the sternal chambers are larger, and the limbs are without dermal ossifications. Their distribution at the present day is world-wide, except in South Africa and the Australian region. The fossil species occur first in the Eocene, and belong for the most part to existing genera.

Patanemys Andrews. Upper Eocene (Barton Clay); England.

Geoemyda Gray (*Geoliemys* Matsumoto). Eocene; Kyûchû, Japan.

Emys Duméril (*Lutremys* Gray) (Fig. 408). Neural bones short, hexagonal; nuchal not distinctly emarginate. Plastron united to the carapace by ligament, and more or less hinged in the adult. Probably Eocene to Recent, though some of the fragmentary fossils referred to this genus may belong to *Clemmys* Wagler and *Ocadia* Gray. *Ocadia* is recorded from the Pliocene of Wadi Natrun, Egypt. *Emys orbicularis* Linn. sp. occurs in the Pleistocene of southern England, below peat in Norfolk, and in peat deposits in southern Sweden.

Chrysemys Gray. Recent and Pleistocene in North America, doubtfully in London Clay (Lower Eocene), England.

Echmatemys Hay. Eocene; North America.

Polyechmatemys Ping. Upper Tertiary; Hopei (Chihli) Province, China.

Graptemys Agassiz. Oligocene to Recent; North America. *Trachemys* Agassiz. Miocene to Recent; North America. *Terrapene* Merrem. Pleistocene and Recent; North America.

Ptychogaster Pomel. Neural bones alternating in size; costals alternately long and short at their inner and outer extremities; nuchal emarginate. Hyoplastrals united to the carapace by suture, the hypoplastrals joining it by a straight ligamentous union, and movable upon a transverse hinge. Oligocene or Lower Miocene; France.

Clemmydopsis Boda. Lower Pliocene; Sopron, Hungary.

[1] *Andrews, C. W.*, *Patanemys bartonensis.* Ann. Mag. Nat. Hist. [9], vol. v., p. 145, 1920.—*Gilmore, C. W.*, Nearly complete Shell of *Trachemys sculpta.* Proc. U.S. Nat. Mus., vol. lxxvii., art. 10, 1930.—*Isberg, O.*, Das ehemalige Vorkommen der Sumpfschildkröte (*Emys orbicularis* L.) in Schweden. Archiv Zool., vol. 21A, no. 3, 1929.—*Newton, E. T.*, Discovery of *Emys lutaria* on the Norfolk Coast. Geol. Mag. [2], vol. vi., p. 304, 1879.—*Staesche, K.*, Sumpfschildkröten aus hessischen Tertiärablagerungen. Abhandl. Hess. Geol. Landesanst., vol. viii., pt. 4, p. 13, 1928.—Schildkröten des Steinheimer Beckens. Palaeontogr., Suppl.-bd. viii., pt. ii.A, 1931.—*Stefano, G. de*, *Emys cuvieri.* Boll. Soc. Zool. Ital. [2], vol. iii., p. 37, 1902.—*Ptychogaster* miocenici della Francia. Palaeont. Ital., vol. ix., p. 61, 1903.

Cistudo Fleming; *Cyclemys* Bell. Recent. *Damonia, Bellia, Nicoria, Hardella, Cachuga* Gray. Pliocene (Siwalik Formation) and Recent in India.

Family 4. **Testudinidae.**[1] (*Chersidae.*) Land Tortoises.

Skull with open temporal fossae; otic notch of quadrate closed behind. Shell completely ossified even in the young, more or less ovoid, and covered with epidermal shields. Plastron suturally united with the marginals; an entoplastron present. Sternal bridge long, sternal chambers very slightly developed; anterior and posterior extremities of hyo- and hypo-plastron little extended inwards; marginals of bridge with median processes interlocking with the rib-ends. Pubic and ischiadic symphyses firmly connected with each other. Limbs with free digits, which are stout and moderately elongate; terminal claws four or five. Second and third digit of pes never with more than two phalanges. Eocene to Recent.

The distribution of the existing *Testudinidae* is nearly the same as that of the *Emydidae.* Gigantic forms of *Testudo* survive on the Galapagos Islands, Aldabra, Mauritius, Seychelles, and Rodriguez.

Cinixys Bell (*Kinixys* Bell; *Cinothorax* Fitz.). Posterior portion of carapace movable in the adult, hinged between the seventh and eighth marginals and the fourth and fifth costals. Gulars distinct. Recent; Africa.

Pyxis Bell. Carapace without hinge; front lobe of plastron mobile. Recent; Madagascar.

Homopus Dum. and Bibr. Carapace and plastron without hinge. Palate without oral ridge. Eocene to Recent. *H. scutella* H. von Meyer sp., from Upper Miocene, Oeningen, Baden.

Achilemys Hay. Middle Eocene (Bridger); Wyoming, U.S.A.

Hadrianus Cope. Distinguished from *Testudo* by the narrow vertebral shields, usually hexagonal neural bones, undivided caudal shield, and more uniform length of extremities of the costal bones. Eocene; North America.

Stylemys Leidy (Fig. 418). Shell with the general characters of *Testudo,* but with all or nearly all of the neural bones hexagonal, with short antero-lateral surfaces; the nuchal not emarginate; posterior caudals not alternating in length; caudal shield undivided. Oligocene to Pliocene; Western United States. *S. nebrascensis* Leidy, the type species, is very abundant in the Oligocene of Dakota, Nebraska, and Wyoming. *S. karakolensis* Riabinin. Lower Tertiary; Turkestan.

Sinohadrianus Ping. Upper Eocene; Honan, China.

Testudo Linn. (*Colossochelys* Falc. and Caut.; *Manouria* Gray; *Xerobates* Ag.). Neural bones alternating in size; costals alternately short and long at their inner and outer extremities; nuchal deeply emarginate. Plastron extensively united with the carapace by suture; buttresses short, never extending

[1] *Burchard, O.,* and *Ahl, E.,* Riesen-Landschildkröten auf Teneriffa. Zeitschr. Deutsch. Geol. Ges., vol. lxxix., Abh., p. 439, 1928.—*Günther, A.,* Gigantic Tortoises. Proc. Linn. Soc. Lond., Sess. 110, p. 14, 1898.—*Lambe, L. M.,* New Species of *Testudo* and *Baena.* Ottawa Nat., vol. xix., p. 187, 1906.—New Species of *Testudo* and a remarkable specimen of *Stylemys nebrascensis. Loc. cit.,* vol. xxvii., p. 57, 1913.—*Loomis, F. B.,* Turtle from the Upper Harrison Beds. Amer. Journ. Sci. [4], vol. xxviii., p. 17, 1909.—*Ping, C.,* New Fossil Land Turtle from Honan. Bull. Geol. Soc. China, vol. viii., p. 231, 1929 (1930).—*Riabinin, A., Testudo turgaica* nov. sp. Trav. Mus. Géol. Acad. Sci. Leningrad, vol. i., p. 53, 1926.—Nouveau Chélonien du Tertiaire inférieur des environs du lac Issyk-koul. Bull. Comité Géol. Leningrad, vol. xlvi., p. 195, 1927. Photographs of Indian *Testudo* (*Colossochelys*) in Natural History (Journ. Amer. Mus. Nat. Hist.), vol. xxxi., p. 183, 1931.

beyond the edge of the costals. Vertebral shields broad, costals very short. Oligocene to Recent. Some Pliocene species attain gigantic size, the shell of *T. perpiniana* Depéret, from the Pliocene of France, having a length of 1·2 m., and that of *T. atlas* Falconer and Cautley sp., from the Pliocene of the Siwalik Hills, India, upwards of 2 m. Other large species occur in the Oligocene of the Fayum, Egypt (*T. ammon* Andrews); in the Lower Miocene of British East Africa (*T. crassa* Andrews); in the Pliocene of Florida; and in the Pleistocene of Southern Spain, Minorca, Teneriffe, Malta, Madagascar, and Argentina.

A *B*

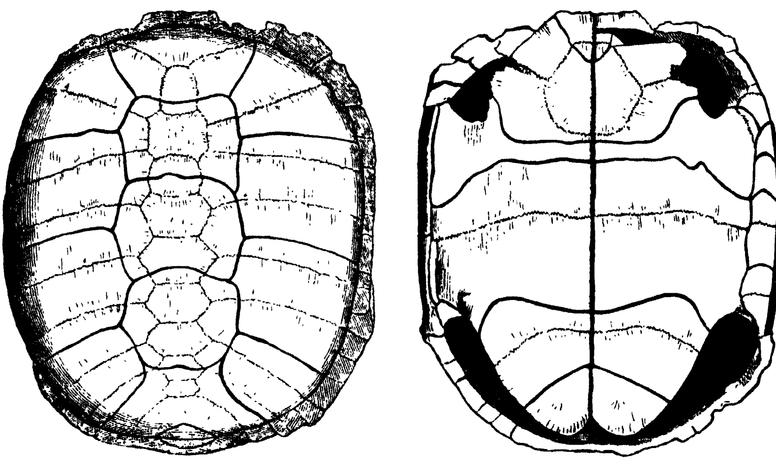


FIG. 418.

Stylemys nebrascensis Leidy. White River Oligocene; South Dakota. *A*, Carapace. *B*, Plastron. 1/3 nat. size (after Leidy).

T. turgaica Riabinin. Miocene; Turga, Siberia. Other species in Miocene or Lower Pliocene of Shensi, China.

Bystra Hay. Upper Tertiary; Holder, Florida, U.S.A.

Family 5. **Cheloniidae.**[1] Marine Turtles.

Roof of temporal region of skull complete; squamosal joining the parietal, and the latter articulating with the postfrontal. Plates from the vomer and palatines usually forming a secondary palate beneath the internal nares. Neck short, head not retractile. Shell more or less incompletely ossified, covered with epidermal shields. Carapace frequently cordiform; nuchal without costiform processes; plastral

[1] *Dollo, L.*, *Eochelone brabantica* et l'évolution des Chéloniens Marins. Bull. Acad. Roy. Belg., Classe Sci., no. 8, p. 1, 1903.—Première Note sur les Chéloniens Landeniens (Éocène inférieur) de la Belgique. Bull. Mus. Roy. Hist. Nat. Belg., vol. iv., p. 129, 1886.—Le genre *Euclastes*. Ann. Soc. Géol. Nord, vol. xv., p. 114, 1888.—*Eosphargis*. Bull. Soc. Belge Géol., vol. xxi., Proc.-Verb., p. 81, 1907.—*Fucini, A.*, La *Chelone sismondai* Portis. Palaeont. Ital., vol. xv., p. 101, 1909.—*Longman, H. A.*, Giant Turtle from the Queensland Lower Cretaceous. Mem. Queensland Mus., vol. iii., p. 24, 1915.—*Misuri, A.*, Nuovo chelonio del calcare miocenico di Lecce (*Euclastes melii* Misuri). Palaeont. Ital., vol. xvi., p. 119, 1910.—*Owen, R.*, Extinct Chelonian Reptile (*Notochelys costata* Owen) from Australia. Quart. Journ. Geol. Soc., vol. xxxviii., p. 178, 1882.—*Rüschkamp, F.*, Schädel von *Allopleuron* (*Chelone*) *Hoffmanni* Gray. Palaeont. Zeitschr., vol. vii., p. 122, 1926.—*Wieland, G. R.*, Structure of the Upper Cretaceous Turtles of New Jersey: *Lytoloma*. Amer. Journ. Sci. [4], vol. xviii., p. 183, 1904.—*Osteopygis* and *Propleura*. *Loc. cit.*, vol. xviii., p. 118, 1904.

bones nine, distinct from the carapace, and with vacuities and digitate lateral extremities. Limbs paddle-shaped, phalanges without condyles, terminal claws reduced to one or two. Supramarginal shields present, and sometimes an intergular. Cretaceous to Recent.

Osteopygis Cope (*Catapleura, Propleura* Cope). Carapace extensively ossified; marginals in eleven pairs. Upper Cretaceous; New Jersey, U.S.A., and Patagonia.

Sinemys Wiman. Lower Cretaceous; Shantung, China.

Cratochelone Longman. Limb bones of giant turtle from Lower Cretaceous of Queensland.

Allopleuron Baur (Fig. 419). Carapace long and narrow, nuchal deeply emarginate, neurals short and wide with a long keel; marginals long and slender. Upper Cretaceous; Maastricht, Holland.

Notochelone Lydekker (*Notochelys* Owen *nec* Gray). Cretaceous; Flinders River, Queensland, Australia.

Peritresius Cope. Shell coarsely sculptured. Upper Cretaceous; New Jersey and Georgia, U.S.A.

Eochelone Dollo. Skull broad and depressed; orbits lateral. Carapace elongated, not keeled. Middle Eocene; Belgium.

Lytoloma Cope (*Euclastes, Puppigerus* Cope; *Glossochelys* Seeley; *Erquelinnesia, Pachyrhynchus* Dollo). Skull resembling that of *Thalassochelys*, very broad and depressed, with orbits far forwards. Carapace rounded posteriorly, vacuities of shell smaller than in *Thalassochelys*; epiplastrals narrow; exposed portion of entoplastron very short; xiphiplastrals uniting extensively in the median line. Upper Cretaceous; New Jersey, U.S.A. Eocene; Belgium and England.

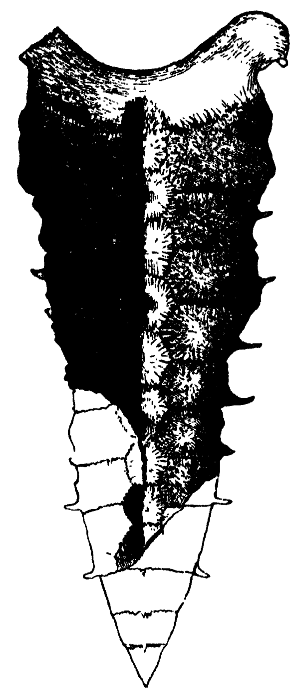


FIG. 419.

Allopleuron hoffmanni Gray sp. Portion of carapace. Upper Cretaceous; Maastricht, Holland. 1/8 nat. size.

Proeretmochelys Dollo. *P. jessoni* Lyd. sp. Cambridge Greensand.

Argillochelys Lydekker. Skull short and wide. Shell and bones of the pectoral arch similar to those of *Thalassochelys*, except that the carapace has but four costal shields, and the xiphiplastrals unite extensively along the median line. Eocene; England.

Eosphargis Lydekker. Skull broad and flat, relatively large; palate as in *Dermochelys*. Carapace much reduced. *E. gigas* Owen sp., with skull 33 cm. in extreme width. Lower Eocene (London Clay and Ypresian); Sheppey and Belgium.

Thalassochelys Fitzinger (*Caretta* Raf.) (Fig. 420). Carapace with vacuities more or less obliterated; at least five pairs of costal shields. A series of inframarginal plastral shields present. Eocene to Recent.

Chelone Brongniart (*Mydas* Gray; *Cimochelys* Owen) (Fig. 406). Skull comparatively long, narrow, with orbits lateral. Shell cordiform or pointed at both ends, with four costal shields, the plastral vacuities persisting for a long period. An intergular and a series of inframarginal shields present. Upper Cretaceous to Recent.

Glyptochelone Dollo. Upper Cretaceous; Limbourg, Belgium. *Lembonax* Cope. Eocene; North America. *Chelyopsis* van Beneden, *Oligochelone* Dollo.

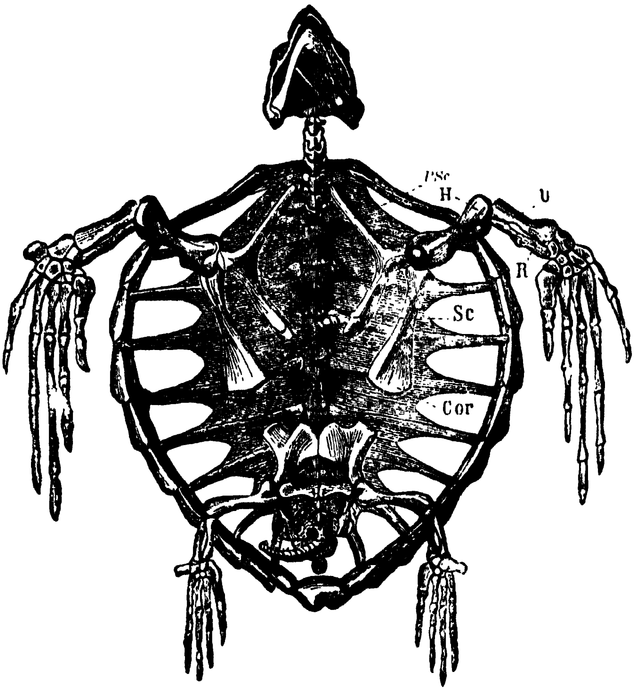


Fig. 420.

Thalassochelys caretta Linn. sp. Ventral aspect of skeleton, the plastron removed. Recent; Mediterranean. *Cor*, coracoid; *H*, humerus; *PSc*, acromion; *R*, radius; *Sc*, scapula; *U*, ulna.

Oligocene; Belgium and Northern Germany. *Syllomus* Cope; *Procolpochelys* Hay. Miocene; North America.

Family 6. **Toxochelyidae.**[1]

As Cheloniidae, *but no secondary palate, fore foot with at least two claws, and phalanges with condyles.* Upper Cretaceous.

According to Hay, the shell is not excavated above the fore limbs as in the *Cheloniidae*, showing that these limbs were not habitually used for swimming.

Toxochelys Cope. Mid-line of carapace with a prominent keel, rising at intervals into tubercles, of which some are distinct dermal bones. Marginals scarcely or not in contact with the ribs. *T. latiremis* Cope, and other species. Upper Cretaceous; Kansas, U.S.A. Perhaps also in Aptian, Hanover.

Cynocercus Cope. Upper Cretaceous; Kansas.

[1] *Oertel, W.*, *Toxochelys gigantea* nov. sp., eine neue Schildkröte aus dem Aptien von Hannover. 7 Jahresb. Niedersächs. Geol. Ver. Hannover, p. 91, 1914.—*Wieland, G. R.*, A new Niobrara *Toxochelys*. Amer. Journ. Sci. [4], vol. xx., p. 325, 1905.

Family 7. **Protostegidae.**[1]

Roof of temporal region of skull complete; parietals with descending plates; no secondary palate. Carapace greatly reduced, but a row of marginals. Plastron very strongly developed and composed of thick ossifications, but with a large median fontanelle. Humerus with the radial process short, blunt, and approximated to the head. Paddles as in Cheloniidae. Upper Cretaceous and Lower Tertiary.

Protostega Cope. Descending parietal plates well developed. Premaxillary beak not prominent; maxilla with broad grinding surface. Carapace intermediate between *Dermochelyidae* and *Cheloniidae*, with several primitive characters regarded as ancestral to both. Plastron with larger bones and a much smaller fontanelle than in *Dermochelys*. Body elongate, the posterior end truncated. Post-axial border of humerus more or less deeply emarginate. *P. gigas* Cope, and other species. Upper Cretaceous; Kansas, U.S.A.

Archelon Wieland (Fig. 421). Larger than the preceding, with a strong premaxillary beak, and the crushing surface of the upper jaw chiefly on the premaxillae. Neural plates very thin, with a row of thin dermal plates above them. Hyoplastra and hypoplastra fringed with numerous digitations. *A. ischyros* Wieland, with carapace nearly 2 metres long and broad. Pierre Cretaceous; South Dakota.

Protosphargis Capellini. Skull unknown. Body skeleton similar to that of *Protostega*, but bones of plastron more slender, and median fontanelle larger. Uppermost Cretaceous; near Verona, Italy.

Pseudosphargis Dames. Skull flat and wide, like that of the *Dermochelyidae*, but with descending parietal processes. Oligocene; Germany.

Family 8. **Dermochelyidae.**[2] (*Athecae* Cope.) Leathery Turtles.

Roof of temporal region of skull complete; parietals without descending plates; parasphenoid very large; no secondary palate. Epidermal shields absent. Carapace of numerous mosaic-like dermal plates, wholly unconnected with the vertebrae and ribs. Plastron without entoplastral bone, usually covered with mosaic of dermal plates. Humerus flattened; limbs paddle-shaped, clawless, the digits of the manus much elongated; phalanges without condyles. Tertiary and Recent.

[1] *Capellini, G.*, Il chelonio Veronese, *Protosphargis veronensis*. Mem. R. Accad. Lincei, Cl. Sci., vol. xviii., p. 291, 1884.—Le Piastre marginali della *Protosphargis veronensis*. Rendic. R. Accad. Sci. Istit. Bologna, vol. ii., p. 97, 1898.—*Case, E. C.*, Osteology and Relationship of *Protostega*. Journ. Morph., vol. xiv., p. 21, 1897.—*Hay, O. P.*, *Protostega*, etc. Amer. Nat., vol. xxxiii., p. 929, 1898.—*Nopcsa, F.*, Becken und Nuchale von *Protosphargis*. Centralbl. f. Min., etc., 1926, Abt. B, p. 285.—*Wieland, G. R.*, *Archelon ischyros*. Amer. Journ. Sci. [4], vol. ii., p. 399, 1896.—Also *loc. cit.*, vol. v., p. 15, 1898; vol. ix., p. 237, 1900; vol. xiv., p. 95, 1902; vol. xv., p. 211, 1903.—Osteology of *Protostega*. Mem. Carnegie Mus., vol. ii., p. 279, 1906.—Revision of the *Protostegidae*. Amer. Journ. Sci. [4], vol xxvii., p. 101, 1909.

[2] *Andrews, C. W.*, New Species of Zeuglodont and of Leathery Turtle from the Eocene of Southern Nigeria. Proc. Zool. Soc., 1919, p. 314, 1920.—*Dollo, L.*, *Psephophorus*. Ann. Soc. Sci. Bruxelles, 1887, p. 1.—Première Note sur les chéloniens oligocènes et néogènes de la Belgique. Bull. Mus. Roy. d'Hist. Nat. Belg., vol. v., p. 59, 1888.—Sur l'origine de la tortue Luth (*Dermochelys coriacea*). Bull. Soc. Roy. Sci. Médic. et Nat. Bruxelles, 1901, p. 1.—*Palmer, W.*, New Species of Leatherback Turtle from the Miocene of Maryland. Proc. U.S. Nat. Mus., vol. xxxvi., p. 369, 1909.—*Seeley, H. G.*, *Psephophorus polygonus* v. Meyer. Quart. Journ. Geol. Soc., vol. xxxvi., p. 406, 1880.—*Versluys, J.*, Affinities of the Leathery Turtle, *Dermochelys coriacea*. Rep. Brit. Assoc. (Birmingham, 1913), p. 791, 1914.—*Völker, H.*, Über das Stamm-, Gliedmassen-, und Hautskelett von *Dermochelys coriacea*. Zool. Jahrb., Anatom. Abth., vol. xxxiii., p. 477 1913.

Cosmochelys Andrews. Tesserae of carapace radially sculptured; only two rows of smaller tesserae between the keeled rows. Rudiments of neural and costal plates beneath. *C. dolloi* Andrews. Lower or Middle Eocene; Ombialla district, S. Nigeria.

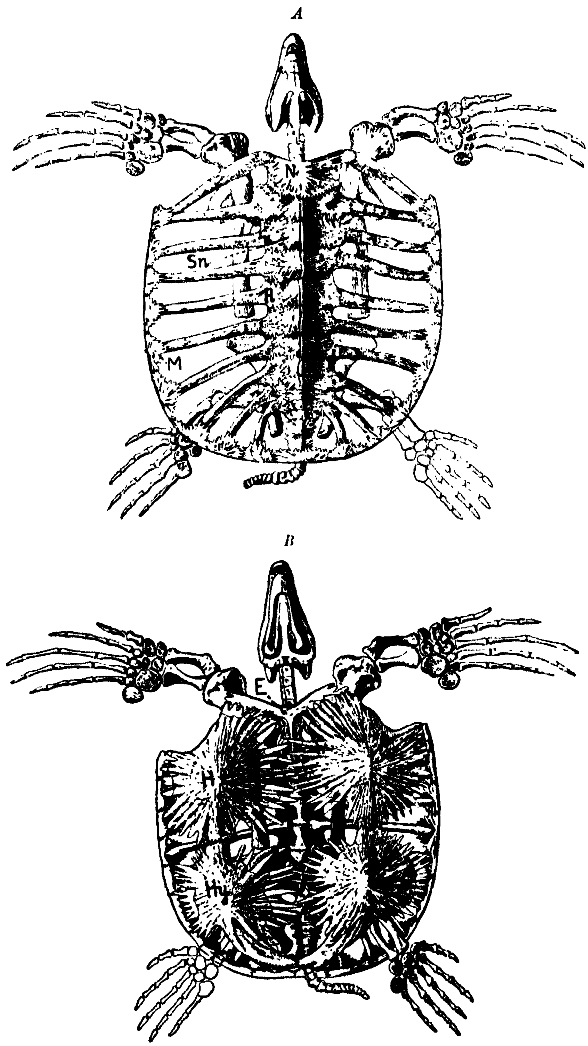


FIG. 421.

Archelon ischyros Wieland. *A*, Dorsal aspect. *B*, Ventral aspect. Upper Cretaceous; South Dakota. *E*, entoplastron; *H*, hyoplastron; *Hy*, hypoplastron; *M*, marginal; *N*, nuchal; *R*, rib; *Sn*, supraneural plate. $1/_{48}$ nat. size (after Wieland).

Psephophorus H. v. Meyer (*Macrochelys* van Beneden *nec* Gray). Skull shorter, thicker, and relatively larger than in *Dermochelys*; shell completely tessellated, sculptured; scutes of the larger longitudinal rows of the carapace without carinae. Eocene to Pliocene; Europe. Upper Eocene; Egypt, and Alabama, U.S.A. Miocene; Maryland, U.S.A.

Dermochelys Blv. (*Sphargis* Merrem). Carapace completely, plastron incompletely bony in the adult, the former with seven, the latter with five keels; tesserae between the keels very numerous; plastral elements eight. Recent; Atlantic, Pacific, and Indian Oceans.

Sub-Order 4. TRIONYCHOIDEA.

Temporal region of skull without roof; descending parieto-pterygoidal processes present. Pterygoids broad throughout, separated from each other, the basisphenoid joining the palatines. Cervical vertebrae without transverse processes. Neck bending by a sigmoid curve in a vertical plane. Sacral and caudal ribs generally attached to well-developed transverse processes of the neural arches. Pelvis free from the carapace and plastron. Neural and costal plates usually forming an incomplete carapace ornamented with coarse vermiculating sculpture; epidermal shields usually absent, when present rudi-

mentary. Feet webbed, the fourth digit with at least four phalanges, and not more than the three inner digits clawed. Marginal plates typically absent, rarely forming an incomplete series, and rarely connected with the ribs. Nine plastral elements; epiplastra separated from the hyoplastra by the Λ-shaped entoplastron.

The group of three-clawed mud turtles appears first in the Upper Cretaceous of North America, and next in the lowest Tertiary strata of both Europe and North America. Some of the ancestral Cretaceous forms have a complete carapace with rudimentary thin epidermal shields, and connect the *Trionychoidea* with the *Cryptodira.* Typical *Trionychidae,* however, occur abundantly in the uppermost Cretaceous formations of North America.

Family 1. **Carettochelyidae.**[1]

Marginal plates present, connected both with the ribs and the reduced plastron; sometimes rudiments of epidermal shields. Eocene to Recent.

Carettochelys Ramsay. Without epidermal shields. Only two claws. Living in New Guinea.

Anosteira Leidy. With thin epidermal shields. Eocene; North America, and Messel, near Darmstadt. Oligocene; Hordwell, England.

Pseudotrionyx Dollo (? *Apholidemys* Pomel). Without epidermal shields. Suture between hypoplastral and xiphiplastral straight. *P. delheidi* Dollo. Middle Eocene; Belgium. Also Lower Eocene (London Clay); Sheppey.

Family 2. **Trionychidae.**[2]

Skull depressed, the small orbits directed more or less upwards and close to the nares; squamosal and supraoccipital with very long posterior processes. Plastron distinct from the carapace, usually with large vacuities; marginal plates absent or rudimentary. Humerus much curved. Upper Cretaceous to Recent.

The existing members of this family are fluviatile, and distributed in the tropical and temperate zones of all the continents except Europe, South America, and Australia.

[1] *Dollo, L.*, Première Note sur les Chéloniens du Bruxellien (Éocène Moyen). Bull. Mus. Roy. d'Hist. Nat. Belg., vol. iv., p. 75, 1886.—*Harrassowitz, H. L. F.*, Eozäne Schildkröten von Messel bei Darmstadt. Centralbl. f. Min., etc., 1919, p. 147. See also Abh. hess. geol. Landesanst., 1922. —*Versluys, J.*, Eine lebende Anosteiride, *Carettochelys insculpta* Ramsay. Palaeont. Zeitschr., vol. v., p. 97, 1922.—*Walther, W. G.*, Die Neu-Guinea-Schildkröte *Carettochelys insculpta* Ramsay. Nova Guinea, vol. xiii., Zool., livr. v., Leiden, 1922.

[2] *Andrews, C. W.*, *Cycloderma.* Quart. Journ. Geol. Soc., vol. lxx., p. 183, 1914.—*Arthaber, G. von*, *Trionyx rostratus*, etc. Beitr. Palaeont. Österr.-Ungarns, vol. xi., p. 179, 1898.—*Gilmore, C. W.*, New Species of *Aspideretes* from the Belly River Cretaceous of Alberta. Trans. Roy. Soc. Canada [3], vol. xvii., sect. iv., p. 1, 1923.—*Heritsch, F.*, Jungtertiäre *Trionyx*-reste aus Mittel-Steiermark. Jahrb. k. k. geol. Reichsanst. Wien, vol. lix., p. 333, 1909.—*Hummel, K.*, Allgemeine Ergebnisse von Studien über fossile Weichschildkröten (Trionychia). Palaeont. Zeitschr., vol. x., p. 53, 1928; also Die fossilen Weichschildkröten (Trionychia). Geol. u. Palaeont. Abhandl., n.s., vol. xvi., pt. 5, 1929.—*Lambe, L. M.*, On *Trionyx foveatus* Leidy and *Trionyx vagans* Cope, from the Cretaceous Rocks of Alberta. Summary Rep. Geol. Surv. Canada, 1901, p. 1, 1902.—*Liebus, A.*, Neue Schildkrötenreste aus den tertiären Süsswassertonen von Preschen bei Bilin in Böhmen. State Geol. Surv. Checoslovak Repub., mem. 4, 1930.—*Misuri, A.*, Nuovo Trionichide dell' arenaria miocenica del Bellunese. Perugia, 1911.—*Negri, A.*, Trionici eocenici ed oligocenici del Veneto. Mem. Soc. Ital. Sci. Napoli, vol. viii., p. 5, 1892.—*Russell, L. S.*, New Species of *Aspideretes* from the Paskapoo Formation of Alberta. Amer. Journ. Sci. [5], vol. xx., p. 27, 1930.—*Sacco, F.*, Trionici di Monte Bolca. Atti R. Accad. Sci. Torino, vol. xxix., p. 654, 1894.—Trionici di Monteviale. *Loc. cit.*, vol. xxx., p. 541, 1895.—*Teppner, W.*, Zur phylogenetischen Entwicklung der protriunguiden Trionyciden des Tertiärs. Centralbl. f. Min., etc., vol. xiv., p. 628, 1914.

Helopanoplia Hay. Laramie (Lance) Cretaceous; Wyoming, U.S.A.

Plastomenus Cope. A preneural plate between the nuchal and first neural. Plastron without median fontanelle. Upper Cretaceous and Lower Eocene; North America.

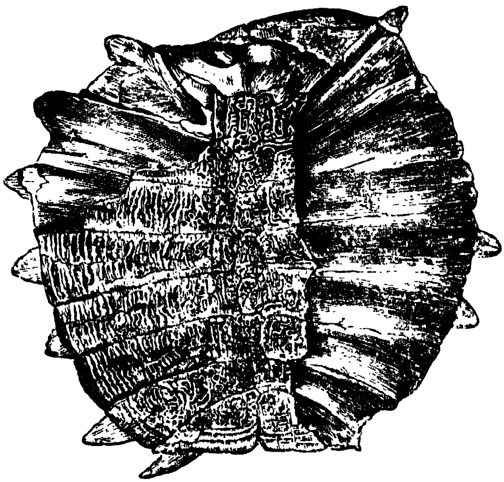


FIG. 422.
Trionyx styriacus Peters. Imperfect carapace and cast of ribs. Miocene lignites; Ebiswald, Styria. 1/4 nat. size (after Peters).

Conchochelys Hay. Jaws with broad crushing surfaces. Puerco Eocene; New Mexico, U.S.A.

Axestemys Hay (*Axestus* Cope). Plastron smooth; nuchal plate partly separated from costals by fontanelles. Eocene (Green River Shales); Wyoming, U.S.A.

Temnotrionyx Hay. Maxilla bearing sharp ridge parallel with cutting edge. Middle Eocene (Bridger); Wyoming, U.S.A.

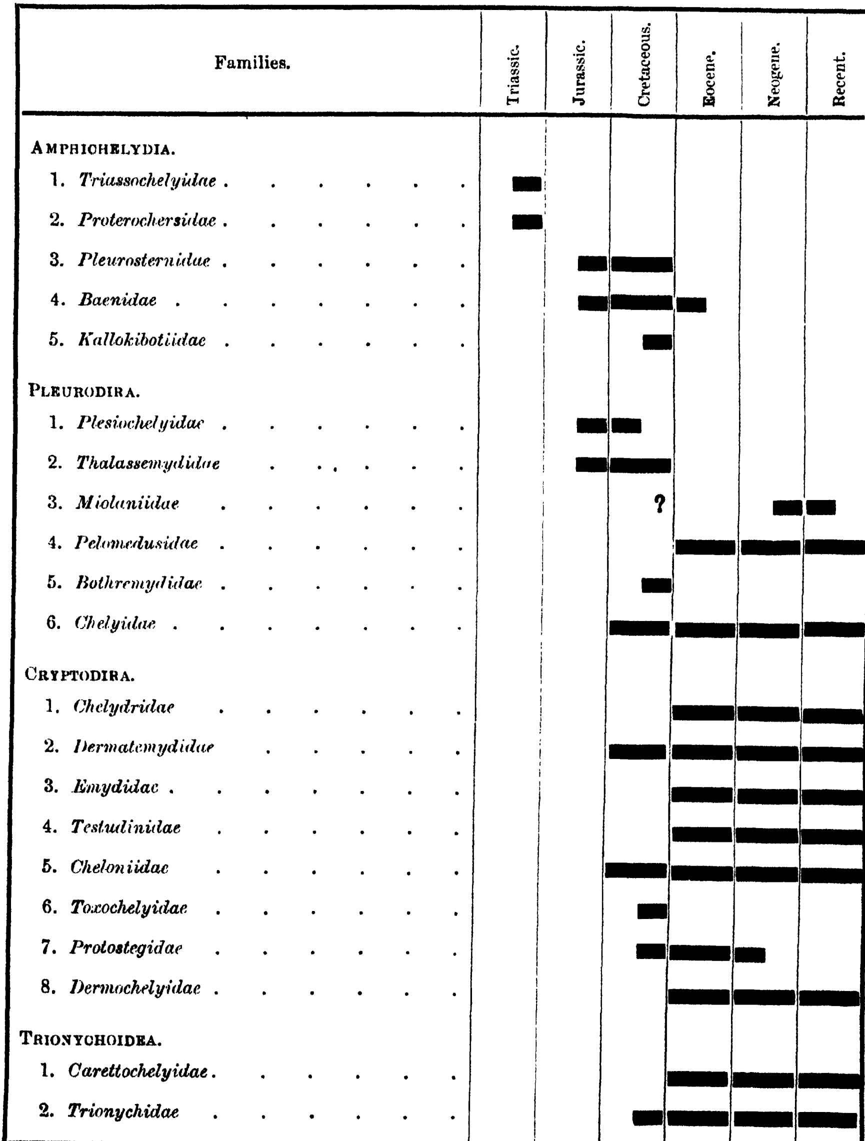
Trionyx Geoffroy (*Amyda* Oken; *Aulacochelys* Lydekker; *Aspideretes* Hay; *Castresia* de Stefano) (Fig. 422). Eight pairs of costal plates, no marginals. Cretaceous and Paleocene forms (*Aspideretes* Hay) with a preneural plate. Found throughout the Tertiary formations, and living in the rivers of Asia, Africa, and North America.

Cycloderma Peters. Miocene to Recent; Africa. *C. victoriae* Andrews. Lower Miocene; near Victoria Nyanza.

Chitra and *Emyda* Gray. Pliocene and Recent; India.

[TABLE

VERTICAL RANGE OF CHELONIA.



Order 9. RHYNCHOCEPHALIA.

Long-tailed, short-necked reptiles, with limbs too feeble for habitual support of the body. Roofing bones of the temporal region of the skull contracting into an upper

and a lower arch; quadrate firmly fixed, buttressed by the pterygoid. Frontal and parietal bones paired. Teeth fused with jaw, rarely in deep sockets; numerous palatal teeth. Vertebrae usually amphicoelous, often with intercentral wedge-bones; cervical ribs double-headed, dorsal ribs single-headed, two vertebrae in sacrum. Pectoral arch with clavicles and interclavicle, elongated scapula, and short and broad perforate coracoid, no ossified precoracoid. Abdominal ribs present in three longitudinal series. All three pelvic bones entering the acetabulum, which is not perforate. Fifth metatarsal much shortened, and somewhat expanded.

The existing genus *Sphenodon* (*Hatteria*) of New Zealand is the sole survivor of an ancient and primitive Order of reptiles which attained its maximum specialisation in the Trias. Most of them, like *Sphenodon*, seem to have been amphibious, spending much time under water. The Jurassic *Pleurosaurus* and *Sapheosaurus* must have been good swimmers; while the Cretaceous *Champsosauridae* and the Triassic *Thalattosauridae* were adapted for life in the open ocean. The earliest known fossil which may belong to the Order is an imperfect skeleton, from the Upper Permian (Kupferschiefer) of Mansfeld, described as *Palaeochamaeleo* Weigelt, with a skull about 6 cm. long. The gently rounded postero-lateral border of the skull, supposed to be formed by the quadrato-jugal, is fringed with a regular row of sharply pointed triangular spines.[1] *Coelurosauravus* Piveteau, with a similarly spiny posterior cranial border, from the Permian of Madagascar, seems to be a nearly related genus.

The body in Rhynchocephalians is lizard-like, long-tailed, sometimes scaly; the vertebral centra are amphicoelous or amphiplatyan, sometimes with persistent notochord, and often with small intercentra (hypocentra). The neural arches are well ossified, and zygapophyses and diapophyses usually conspicuous. Most of the cervical ribs are double-headed, all those of the trunk single-headed; sometimes the latter bear uncinate processes. Three longitudinal series of abdominal ribs occur between the limb girdles, and correspond to the ventral armouring of Stegocephalians.

The *skull* (Fig. 339, p. 236) is remarkable for the large size of the orbits and temporal vacuities. The upper temporal arch is formed by the postorbital and squamosal, the lower arch by the quadrato-jugal and jugal. The quadrate is always fixed, and buttressed by the pterygoids, which extend forwards to the vomer. In the *Rhynchosauridae* F. von Huene identifies a narrow tabular bone at the hinder lateral angle of the skull. The brain cavity is of small size, and roofed by the narrow parietals, between which and the pterygoids is a vertical columella (epipterygoid). A pineal foramen is often present. The external nares are almost terminal in position, except in the *Thalattosauridae* in which the premaxillae are elongated. Vomers, palatines, and pterygoids together form an extensive bony palate. Acrodont teeth occur in regular series on the narrow premaxillae, maxillae, and mandible, and on various bones of the palate. Occasionally the teeth are inserted in shallow alveoli, and very rarely are absent altogether.

The *pectoral arch* is incompletely ossified. The scapula is represented by an elongated rectangular bone, and the inner border of the small elliptical coracoids remains cartilaginous. The clavicle is a slender bent rod connecting the scapula with a large rhomboidal or T-shaped interclavicle, which overlies the cartilaginous sternum. The distal end of the humerus is pierced in the

[1] *Huene, F. von, Palaeochamaeleo* und *Coelurosauravus.* Centralbl. f. Min., etc., 1930, Abt. B, p. 440.—*Weigelt, J., Palaeochamaeleo jaekeli* nov. gen. nov. sp. Leopoldina (Halle), vol. vi., p. 625, 1930.

fossil forms by an entepicondylar foramen or groove, but in *Sphenodon* both entepicondylar and ectepicondylar foramina occur. In general the articular surfaces of the humerus, radius, and ulna are not completely ossified. Five distinct elements occur in the distal row of the carpus, and two centralia are often present. The feet are five-toed, and the phalangeal formula of *Sphenodon* is 2, 3, 4, 5, 3 (4).

The *pelvic arch* consists of a small, nearly vertical ilium, a discoidal pubis with obturator notch, and a somewhat expanded ischium, which remains separated from the pubis. Both pubis and ischium are imperfectly ossified among the earlier forms. The hind limb is somewhat longer than the fore limb, and resembles that of Lacertilians.

Family 1. **Rhynchosauridae.**[1]

Skull short and broad, with a beak-like rostrum formed by the slender, toothless premaxillae; external narial opening single, terminal; no pineal foramen; teeth low, conical, or pyramidal, in one or more rows on the tooth-bearing bones. Pubis and ischium in form of extended plates. Triassic.

Rhynchosaurus Owen. Skull slightly longer than broad; the slender rostrum sharply curved downwards; the large orbits partly directed upwards, with everted rims, suggesting aquatic habits. Splenials entering the toothless mandibular symphysis. A single row of teeth on the dentary, probably also on the maxilla and palatine. Vertebrae deeply amphicoelous, seven or eight cervicals and about fifteen rib-bearing trunk vertebrae; intercentra not observed. Ribs without uncinate processes. Hind limb larger than fore limb and femur sigmoidally bent. Covered with polygonal or irregularly rhombic epidermal scales, each with a slight central boss. *R. articeps* Owen, with skull 6 to 7 cm. in length, known by skeletons lacking only tail. Keuper; Grinsill, Shropshire. Footprints in Keuper of other English localities (*Rhynchosauroides* Maidwell emend. Nopcsa). *Antipus* Hitchcock. Similar footprints. Triassic; Massachusetts.

Hyperodapedon Huxley (*Parasuchus* Huxley) (Fig. 423). Skull at least as broad as long, with rostrum sharply curved downwards. Two or more rows of teeth on maxilla and on palatine. About twenty-four presacral vertebrae, of which six or seven are cervical. *H. gordoni* Huxley, known by stout skeleton about 2 m. long. Upper Triassic; Elgin, Scotland. Fragments of other species in Trias of Devonshire, Warwickshire, and the Maleri Beds of central India.

Stenometopon Boulenger. Premaxillary rostrum not curved downwards, nasal bones reduced or absent. Upper Triassic; Elgin, Scotland.

Scaphonyx A. S. Woodward. Skull about as long as broad, with rostrum

[1] *Boulenger, G. A.*, Reptilian Remains from the Trias of Elgin. Phil. Trans. Roy. Soc., vol. cxcvi. B, p. 175, 1904.—*Broom, R.*, *Howesia.* Proc. Zool. Soc., 1906, p. 591.—*Haughton, S. H.*, Skull and partial Skeleton of *Mesosuchus browni* Watson. Trans. Roy. Soc. S. Africa, vol. xii., p. 17, 1925.—*Huene, F. von*, Gondwana-Reptilien in Südamerika [revised in following memoir, 1929]. Palaeontologia Hungarica, vol. ii., p. 1, 1926.—Rhynchosaurier und andere Reptilien aus den Gondwana-Ablagerungen Südamerikas. Geol. u. Palaeont. Abhandl., n.s., vol. xvii., p. 1, 1929.—*Huxley, T. H.*, *Hyperodapedon.* Quart. Journ. Geol. Soc., vol. xxv., p. 138, 1869; and *loc. cit.*, vol. xlii., p. 675, 1887.—*Watson, D. M. S.*, Skull of *Rhynchosaurus.* Rep. Brit. Assoc., 1909, p. 155, 1910.—*Mesosuchus browni.* Rec. Albany Mus., vol. ii., p. 296 [revised by Broom in Proc. Zool. Soc., 1913, p. 627].—*Woodward, A. S.*, *Rhynchosaurus articeps* (Owen). Rep. Brit. Assoc., 1906, p. 293, 1907.

sharply curved downwards, and teeth of maxilla and palatine in more than one series. Not yet defined. Also *Cephalonia*, *Cephalastron*, *Cephalastronius*, and *Scaphonychinius* F. von Huene. Triassic; Santa Maria, Rio Grande do Sul, Brazil.

? *Eifelosaurus* Jaekel. Bunter Sandstone; Eifel, Germany.

? *Gampsodactylum* Nopcsa.

According to S. H. Haughton and F. von Huene, the following genera belong to a distinct but closely related family also with a single external narial opening:

Howesia Broom. Rows of teeth on dentary, maxilla, and pterygoid, but palatine apparently toothless. Rudimentary pineal foramen. Karroo Formation (*Cynognathus* Zone); Aliwal North, S. Africa.

Mesosuchus Watson emend. Broom. Two teeth in premaxilla. Jugal slightly separated from quadratojugal, leaving gap in lower temporal arch. Small pineal foramen. Karroo Formation; Aliwal North.

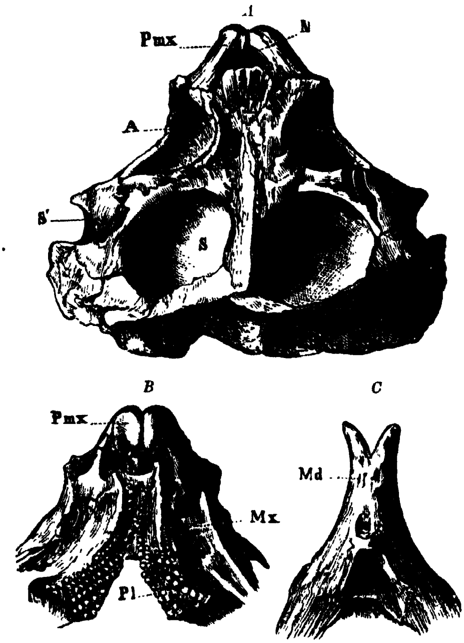


Fig. 423.

Hyperodapedon gordoni Huxley. *A*, Upper aspect of skull. *B*, Palate. *C*, Mandibular symphysis from below. Upper Trias; Elgin, Scotland. *A*, orbit; *Md*, mandibular fork; *Mx*, maxilla; *N*, narial opening; *Pl*, palatine; *Pmx*, premaxilla; *S*, supratemporal vacuity; *S'*, lateral temporal vacuity. 1/4 nat. size (after Huxley).

Family 2. **Sphenodontidae.**[1]

Premaxillae forming beak-like rostrum; external narial opening paired, far forwards; a pineal foramen; a coronoid process in mandible; teeth in one row on the maxilla, palatine, and dentary. Vertebrae amphicoelous, with numerous intercentra. Pubis and ischium less primitive than in the Rhynchosauridae. Triassic to Recent.

Brachyrhinodon F. von Huene. Rostrum comparatively short, orbits very

[1] *Ammon, L. von, Homoeosaurus maximiliani.* Abhandl. k. bayer. Akad. Wiss., math.-naturw. Cl., vol. xv., p. 499, 1885.—*Andreae, A., Acrosaurus frischmanni.* Bericht Senckenberg. Naturforsch. Ges. Frankfurt, 1893, p. 21.—*Barbour, T. H.*, and *Stetson, H. C.*, Squamation of *Homoeosaurus.* Bull. Mus. Comp. Zool. Harvard, vol. lxix., p. 99, 1929.—*Boulenger, G. A.*, Sur le genre *Saphaeosaurus.* Comptes Rendus Acad. Sci. Paris, vol. 169, p. 605, 1919.—*Broili, F.*, Ein neuer Fund von *Pleurosaurus.* Abhandl. Bayer. Akad. Wiss., math.-naturw. Abt., vol. xxx., 8 Abh., 1926.—*Dames, W.*, Gattung *Pleurosaurus.* Sitzb. k. preuss. Akad. Wiss., vol. xlii., p. 1107, 1896.—*D'Erasmo, G., Chometokadmon.* Palaeont. Italica, vol. xxi., p. 47, 1915.—*Gilmore, C. W.*, New Rhynchocephalian from Jurassic of Wyoming. Proc. U.S. Nat. Mus., vol. xxxvii., p. 35, 1909.—*Günther, A.*, Anatomy of *Hatteria.* Phil. Trans. Roy. Soc., vol. clvii., p. 595, 1867.—*Howes, G. B.*, and *Swinnerton, H. H.*, Development of Skeleton of *Sphenodon.* Trans. Zool. Soc., vol. xvi., p. 1, 1901.—*Huene, F. von, Brachyrhinodon taylori.* Neues Jahrb. f. Min., etc., 1910, vol. ii., p. 29; also *loc. cit.*, 1912, vol. i., p. 51.—*Lortet, L.*, Reptiles fossiles du bassin du Rhône. Archives Mus. Hist. Nat. Lyon, vol. v., p. 1, 1892.—*Simpson, G. G.*, American Terrestrial Rhynchocephalia. Amer. Journ. Sci. [5], vol. xii., p. 12, 1926.—*Strunz, C.*, Die Präparation eines *Pleurosaurus* Skeletts. Natur u. Museum, Frankfurt, vol. lvii., p. 116, 1928.—*Watson, D. M. S., Pleurosaurus.* Ann. Mag. Nat. Hist. [8], vol. xiv., p. 84, 1914.

large. About twenty-five presacral vertebrae. *B. taylori* Huene, about 20 cm. long. Upper Triassic; Elgin, Scotland.

Polysphenodon Jaekel. Middle Keuper; Hanover.

Palacrodon Broom. Upper Beaufort Beds (*Cynognathus* Zone); South Africa.

Homoeosaurus H. v. Meyer (Fig. 424). Differing from the Recent *Sphenodon* in absence of intercentra, dorsal ribs without uncinate processes, and humerus not pierced by an entepicondylar foramen. Mandibular rami united at the symphysis by ligament; sclerotic ring present; about twenty-five presacral vertebrae; second sacral rib bifid distally. According to Barbour and Stetson the scales are similar to those on the regenerated tail of *Sphenodon*. *H. maximiliani* v. Meyer and other species from 20 to 40 cm. long. Upper Jurassic (Lithographic Stone); Bavaria. Kimmeridgian of Hanover, and Purbeckian of England.

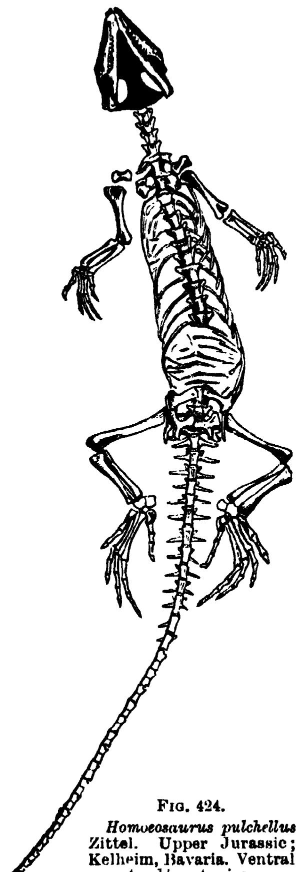


Fig. 424.
Homoeosaurus pulchellus Zittel. Upper Jurassic; Kelheim, Bavaria. Ventral aspect. 1/2 nat. size.

Megasaurus Vidal. Upper Jurassic; Montsech, Lérida, Spain.

Ardeosaurus H. v. Meyer. Upper Jurassic (Lithographic Stone); Bavaria.

Pleurosaurus H. v. Meyer (*Anguisaurus* Münster; *Saurophidium* Jourdan). Body serpentiform, the tail forming two-thirds the total length. Snout tapering in front. The skull is always much crushed, and the temporal region has not yet been satisfactorily observed. About fifty presacral vertebrae, of which eight or nine are cervical; about 120 caudal vertebrae. Fore limbs shorter than the hinder pair, both small. *P. goldfussi* H. v. Meyer and *P. muensteri* Wagner sp. about 1·5 m. long. Upper Jurassic (Lithographic Stone); Bavaria, and Cerin, France.

Acrosaurus H. von Meyer may be the young of *Pleurosaurus*.

Opisthias Gilmore; *Theretairus* Simpson. Lower jaws from Upper Jurassic (Morrison Formation); Como Bluff, Wyoming.

Chometokadmon Costa. One known specimen shows a regenerated tail. Neocomian; Pietraroja, Benevento, Italy.

Sphenodon Gray (*Hatteria* Gray) (Fig. 339). Inferior border of the large orbits formed by maxilla; a single tooth on either side of the premaxillary beak; twenty-five presacral vertebrae; intercentra present between all the vertebrae; ribs with uncinate processes; humerus with both entepicondylar and ectepicondylar foramina or grooves. Recent, inhabiting certain islands off New Zealand.

The following genus may belong to a distinct family:

Sapheosaurus H. v. Meyer (*Piocormus* Wagner; *Sauranodon* Jourdan). Jaws toothless, probably sheathed with horn. Pineal foramen not observed. About twenty-five presacral vertebrae, supposed to be procoelous. *S. thiollierei*

H. v. Meyer about 60 cm. long. Upper Jurassic (Lithographic Stone); Cerin, France.

The two following families are of marine Rhynchocephalians. The *Champsosauridae* are referred by Cope to a special Sub-Order *Choristodera*, and the *Thalattosauridae* are regarded by Merriam as forming a distinct Order *Thalattosauria*.

Family 3. **Champsosauridae.**[1]

Skull with elongated gavial-like snout, and terminal single narial opening into which the nasal bones enter; no pineal foramen; no coronoid process in mandible; splenial entering elongated mandibular symphysis. A single series of large conical teeth, fluted at the base, on margin of the jaws, and irregular longitudinal series of minute teeth on the vomers, palatines, pterygoids, and transverse bones. Vertebral centra completely ossified, slightly biconcave or amphiplatyan, and suturally united with their neural arches; intercentra only between the cervical vertebrae. Interclavicle T*-shaped. No vacuity between pubes and ischia. Apparently no scales.* Cretaceous and Lower Eocene.

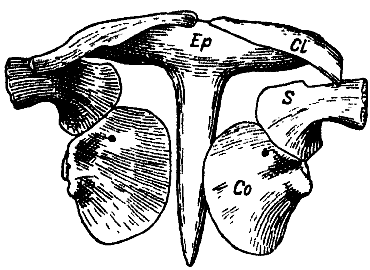


Fig. 425.
Champsosaurus laramiensis Brown. Pectoral arch from above. Upper Cretaceous (Laramie); Montana. *Cl*, clavicle; *Co*, coracoid; *Ep*, interclavicle; *S*, scapula. $^1/_3$ nat. size (after Brown).

Champsosaurus Cope (Fig. 425). External narial opening bounded by premaxillae and fused nasals. Maxilla excluded from lower border of orbit. Forty teeth in each ramus of mandible. Twenty-six presacral vertebrae, and first caudal with sacral ribs. Humerus with ectepicondylar groove instead of foramen. Upper Cretaceous and Lower Eocene of North America.

Simoedosaurus Gervais. Maxilla entering external narial opening and also lower border of orbit. Sixty teeth in each ramus of mandible. Only two vertebrae with sacral ribs. *S. lemoinei* Gervais and other species up to 2·5 m. in length. Upper Cretaceous and Lower Eocene of N. France and Belgium.

Fragments of a Champsosaurian also occur in a deep-sea Cretaceous deposit in the Island of Timor, E. Indies.

Family 4. **Thalattosauridae.**[2]

Skull with premaxillae forming elongated snout, and paired narial opening close to the large orbits; a ring of sclerotic plates; a pineal foramen; a coronoid process in mandible; splenials not entering mandibular symphysis. Teeth on margin of

[1] *Brown, B.*, Osteology of *Champsosaurus*. Mem. Amer. Mus. Nat. Hist., vol. ix., p. 1, 1905.—*Dollo, L.*, Première Note sur le Simoedosaurien d'Erquelinnes. Bull. Mus. Roy. Hist. Nat. Belg., vol. iii., p. 151, 1884.—Nouvelle Note sur le Champsosaure. Bull. Soc. Belge Géol., etc., vol. v., Mém., p. 5, 1891.—*Parks, W. A.*, *Champsosaurus albertensis*. Univ. Toronto Studies, Geol. Ser., no. 23, 1927.

[2] *Merriam, J. C.*, The *Thalattosauria*. Mem. California Acad. Sci., vol. v., p. 1, 1905.—Thalattosaurian Genus *Nectosaurus*. Bull. Dept. Geol. Univ. California, vol. v., no. 13, 1908.

jaws, vomers, and pterygoids. Vertebral centra completely ossified, amphicoelous, and suturally united with their neural arches; intercentra not observed. Limbs paddle-shaped. Triassic.

Thalattosaurus Merriam (Fig. 426). Teeth in premaxillae and anterior end of mandible slender, conical, in deep pits; hinder mandibular teeth elliptical, low-crowned, for crushing. Teeth in maxillae and pterygoids conical, in vomers bluntly conical. Premaxillae, maxillae, and dentaries with sculptured external ornament. *T. alexandrae* Merriam (Fig. 426), about 2 m. in length, the skull about 30 cm. long. Upper Triassic; Shasta Co., California.

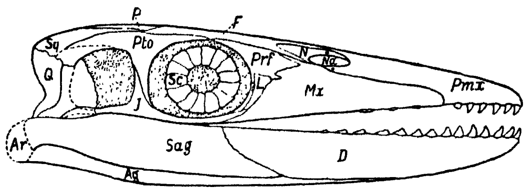


Fig. 426.

Thalattosaurus alexandrae Merriam. Skull and mandible restored in right side view. Upper Triassic; California. *Ag*, angular; *Ar*, articular; *D*, dentary; *F*, frontal; *J*, jugal; *L*, lachrymal; *Mx*, maxilla; *N*, nasal; *Na*, narial opening; *P*, parietal; *Pmx*, premaxilla; *Prf*, prefrontal; *Pto*, postorbito-frontal; *Q*, quadrate; *Sag*, surangular; *Sc*, sclerotic plates; *Sq*, squamosal. 1/4 nat. size (after Merriam).

Nectosaurus Merriam. Same formation and locality.

VERTICAL RANGE OF RHYNCHOCEPHALIA.

Families.	Triassic.	Jurassic.	Cretaceous.	Eocene.	Neogene.	Recent.
1. *Rhynchosauridae*	■					
2. *Sphenodontidae*	■	■	■	■	■	■
3. *Champsosauridae*			■	■		
4. *Thalattosauridae*	■					

Order 10. SQUAMATA. (*Lepidosauria, Streptostylica.*)

Roofing bones of temporal region of skull reduced to one upper arch, or not forming any arch; quadrate movable. Narial opening paired; septomaxillae present; premaxillae fused; usually a pineal foramen; palatal vacuities large, and pterygoids not reaching vomer; teeth acrodont or pleurodont. Body more or less elongated, covered with horny scales, rarely with bony scutes. Vertebrae usually procoelous, rarely amphicoelous; not more than two sacrals. Ribs single-headed, articulating with centra; abdominal ribs absent or rudimentary, No ossified precoracoid. In pelvis, when present, upper end of ilium rod-shaped, and pubis pierced by an obturator foramen. Limbs sometimes reduced or absent.

This Order comprises Lizards, Snakes, and an extinct group of aquatic reptiles, the *Pythonomorpha*; and the earliest clearly recognised members occur in the Cretaceous. The *Squamata* are evidently closely allied to Rhynchocephalians, with which they may have had a common origin.

Sub-Order 1. LACERTILIA. Saurii. Lizards.[1]

Scaly, long-tailed reptiles, with elongated and sometimes serpentiform body. Superior temporal arch sometimes wanting, and quadrate loosely attached to cranium. Columella (epipterygoid) rod-like or rudimentary; alisphenoid and orbitosphenoid not ossified. Mandibular rami suturally united at symphysis; teeth acrodont or pleurodont. Sternum usually, and limb girdles always present, but one or both pairs of limbs sometimes wanting. Limbs for walking, and usually provided with five clawed digits.

The majority of lizards possess a dermal covering of horny or in some cases of bony scales, scutes, or spines, extending over the head and whole of the body. The vertebral column consists of numerous procoelous vertebrae (amphicoelous only among the *Geckonidae* and *Uropeltidae*), in which the neural arches are coössified with their centra. There are seldom more than nine cervicals, and the atlas is composed of two dorsal pieces, either separate or united, and one ventral piece in the form of a free hypapophysis or intercentrum. Both the cervical and dorsal series have the transverse processes weakly developed, so that the ribs appear attached by a short tubercle. All the ribs are single-headed. They are wanting on the anterior cervicals, some of the lumbar, and all of the caudal vertebrae. The sacrum is composed of two vertebrae. Stout transverse processes and chevron bones are borne by the caudals.

A sternum is present, although sometimes rudimentary, in all lizards except *Amphisbaena*; it usually occurs as a large rhombic or shield-shaped bone, sometimes pierced by two foramina. The ventral portions of the anterior dorsal ribs which join the sternum are sometimes cartilaginous, and in other cases bony.

The *skull* (Fig. 427) is distinguished from that of Rhynchocephalians chiefly by its large free quadrate, a delicate rod-like columella (epipterygoid),

[1] *Boulenger, G. A.*, Les Affinités et la dispersion géographique des Lacertides. Comptes Rendus Acad. Sci. Paris, vol. 166, p. 594, 1918.—Les Lézards hélodermatides de l'Éocène supérieur de la France. *Loc. cit.*, p. 889.—*Cope, E. D.*, The Vertebrata of the Tertiary Formations of the West. Rep. U.S. Geol. Surv. Territ., vol. iii., 1883.—Osteology of the Lacertilia. Proc. Amer. Phil. Soc., vol. xxx., p. 185, 1892.—*Dollo, L.*, *Saniwa orsmaelensis*. Bull. Soc. Belge Géol., etc., vol. xxxiii., p. 76, 1923.—*Douglass, E.*, Some Oligocene Lizards. Ann. Carnegie Mus., vol. iv., p. 278, 1908.—*Fejérváry, G. J. de*, Fossil *Varanidae* and *Megalanidae*. Ann. Mus. Nat. Hungar., vol. xvi., p. 341, 1918.—*Gilmore, C. W.*, New Description of *Saniwa ensidens* Leidy. Proc. U.S. Nat. Mus., vol. 60, art. 23, 1922.—Lizard Skull from the Oligocene of Nebraska. Univ. Kansas Sci. Bull., vol. xvi., p. 229, 1926.—Fossil Lizards of North America. Mem. Nat. Acad. Sci., vol. xxii., no. 3, 1928.—*Marsh, O. C.*, On *Glyptosaurus*, *Tinosaurus*, etc. Amer. Journ. Sci. [3], vol. i., p. 456, 1871; and *loc. cit.*, vol. iv., p. 298, 1872.—*Meyer, H. von*, Lacerten aus der Braunkohle des Siebengebirges. Palaeontogr., vol. vii., p. 74, 1860.—*Nopcsa, F.*, Zur Kenntnis der fossilen Eidechsen. Beitr. Paläont. u. Geol. Österreich-Ungarns, vol. xxi., p. 33, 1908 (with bibliography).—*Parker, W. K.*, On the structure and development of the skull in the Lacertilia. Phil. Trans. Roy. Soc., vol. clxx., 1880.—*Seeley, H. G.*, *Patricosaurus merocratus*, Seeley, a Lizard from the Cambridge Greensand. Quart. Journ. Geol. Soc., vol. xliii., p. 216, 1887.—*Stefano, G. de*, I sauri del Quercy. Atti Soc. Ital. Sci. Nat., vol. xlii., p. 382, 1904.—*Weigelt, J.*, *Placosaurus waltheri* n. sp. Jahrb. Halleschen Verband. z. Erforsch., etc., n.s., vol. viii., 1929.

and the constant absence of a lower, and occasional absence of an upper temporal arch. The vomer is unpaired, and not in contact with the pterygoids; and the latter, together with the palatines, form a flat thin palate pierced by large vacuities. A transverse bone (ectopterygoid) occurs between the maxillae and pterygoids. The external nares are separate, and commonly placed near the orbits. The opisthotic is fused with the exoccipital, forming the so-called parotic process of the posterior temporal region. The distal end of this process serves with the posterior ends of the squamosal and supratemporal (sometimes named tabular) as a buttress to which the movable quadrate is

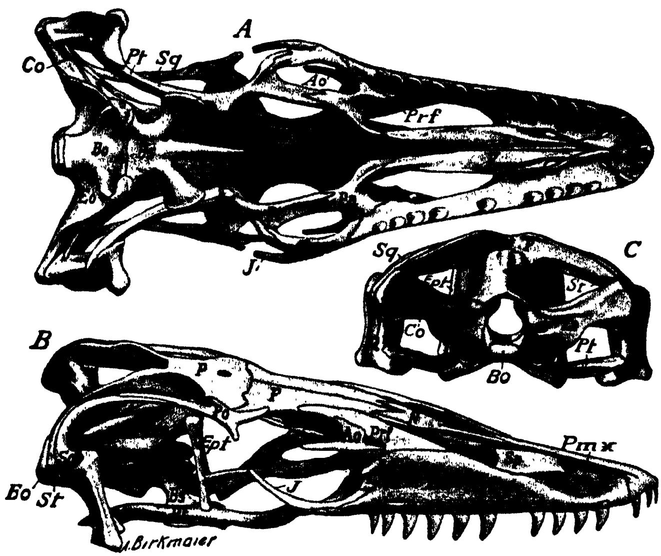


Fig. 427.

Skull of *Varanus*, in palatal (*A*), right lateral (*B*), and occipital (*C*) view. Recent; Africa. *Ao*, supraorbital; *Bo*, basioccipital; *Bs*, basisphenoid; *Co*, stapes (columella auris); *Eo*, exoccipital; *Ept*, epipterygoid (columella); *F*, frontal; *L*, lachrymal; *Mx*, maxilla; *N*, nasal; *P*, parietals with pineal foramen; *Pa*, palatine; *Pmx*, premaxilla; *Po*, postfrontal (postorbital); *Prf*, prefrontal; *Pro*, prootic; *Pt*, pterygoid; *Q*, quadrate; *So*, supraoccipital; *Sp*, septomaxilla; *Sq*, squamosal; *St*, supratemporal or tabular; *Tr*, transverse; *V*, vomer.

attached. The supratemporal itself is of small size and situated between the outer angle of the parietal and distal end of the squamosal. The postorbito-frontal unites with the forward end of the squamosal to form the lower border of the superior temporal fossa, and also sometimes unites with the jugal to form with this bone the posterior border of the orbit. In lizards the jugal is never in direct connection with the quadrate. A pineal foramen occurs, and the parietal is frequently unpaired.

The mandibular rami (Fig. 428) are suturally united at the symphysis; they exhibit the same structure as in Pythonomorphs, except that there is no movable articulation behind the middle of each ramus. Teeth are always present in upper and lower jaws, and occur rarely on the palatines, pterygoids, and vomer. They are either acutely or obtusely conical, chisel- or arrowhead-shaped, serrated or carinated on the anterior and posterior edges, or in some cases their form may be hemispherical. Their bases are completely fused with the supporting bone, and their arrangement is either acrodont or pleurodont.

Successional teeth are developed on the inner side of the functional teeth, and gradually displace them.

As a rule two pairs of limbs provided with five clawed digits are present, although the hinder pair may be rudimentary, and in some cases both pairs are wanting. The limb girdles persist, however, even among apodal forms, but the pelvic arch may become reduced. The coracoid is relatively large, and develops an anterior process, or precoracoid. The scapula also consists of two portions, of which the distal (suprascapula) is the larger and usually remains cartilaginous. The scapula proper is in some cases bifid at its distal extremity. The rod-shaped clavicle connects the anterior border of the scapula with the T-shaped or cruciform interclavicle, which is situated in

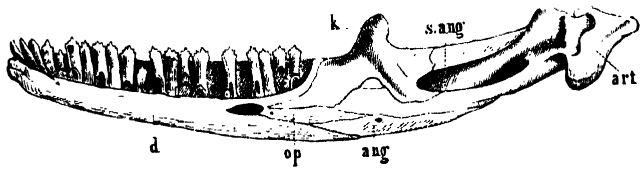


FIG. 428.

Iguana tuberculata Laur. Recent; West Indies. Inner aspect of right ramus of mandible, showing pleurodont teeth. *ang*, angular; *art*, articular; *d*, dentary; *k*, coronoid; *op*, splenial; *s.ang*, surangular. (After Cuvier.)

front of the sternum. The bones of the fore limb resemble those of Rhynchocephalians, except that the humerus never displays distal foramina. There are eight small carpals arranged in two rows, and the usual phalangeal formula is 2, 3, 4, 5, 3.

Where the hind limb is normally developed, the ilia are movably attached to the cartilaginous ends of the sacral ribs. Pubes and ischia meet in a ventral symphysis, and the anterior border of the former frequently develops a strongly curved process. The femur generally exceeds the humerus in length, and the bones of the crus remain separate. The proximal tarsals consist of a large tibiale (astragalus) and fibulare (calcaneum); there are often but two free tarsals present in the distal row (nos. III. and IV.), the remainder being fused with the metatarsals. The phalangeal formula of the pes is usually 2, 3, 4, 5, 4.

Lizards of the present day are restricted almost exclusively to the tropical and temperate zones. The known fossil forms are few. The oldest remains commonly associated with lizards are the imperfect skeletons of *Euposaurus* Lortet from the Upper Jurassic (Lithographic Stone) of Cerin (Ain), France, and the fragmentary jaws and procoelous vertebrae from the English Purbeckian, known as *Macellodus brodiei* Owen and *Saurillus obtusus* Owen, but these are too imperfect for accurate determination. The jaws from the Morrison Formation of Wyoming named *Cteniogenys* Gilmore, from the supposed Lower Cretaceous of Jujuy, Argentina, named *Carlesia* F. von Huene, and from the Upper Cretaceous (Lance or Laramie) of Wyoming named *Chamops* Marsh and *Parasaniwa* Gilmore, seem to be Lacertilian; perhaps also the Upper Cretaceous jaws named *Alethesaurus*, *Habrosaurus*, *Lanceosaurus*, *Odaxosaurus*, *Prionosaurus* Gilmore, and the detached vertebrae and other fragments named *Megasaurus*, *Harpagosaurus* Gilmore. There are also two families of aquatic lizards of Cretaceous age known by nearly complete skeletons.

Family 1. **Dolichosauridae.**[1]

Small, aquatic, serpentiform reptiles, with reduced lizard-like limbs and limb-arches. Rami of mandible united by suture at symphysis. No sclerotic plates. Teeth pleurodont, only on margin of jaws. Head small and neck elongated, with not less than thirteen vertebrae. Vertebrae procoelous, and articulated both by zygapophyses and a zygosphene-zygantrum. Sacral vertebrae not anchylosed. No abdominal ribs. Fore limbs shorter than hind limbs. Cretaceous.

The *Dolichosauridae* are small aquatic lizards, with small limbs and a long swimming tail, found in European marine Cretaceous deposits. Many of the detached vertebrae of Cretaceous age, commonly classed as Ophidian, are doubtless Dolichosaurian.

Dolichosaurus Owen. About fifty-seven presacral vertebrae; slender cervical ribs. Pectoral arch, including sternum, well ossified. Articular ends of stout limb bones not ossified. *D. longicollis* Owen, about 80 cm. in length, from English Lower Chalk (Upper Cretaceous).

Adriosaurus Seeley. About thirteen cervical, twenty-seven trunk, two sacral, and sixty-seven caudal vertebrae; no cervical ribs. *A. suessi* Seeley, about 35 cm. in length, with proportion of fore to hind limb 11 : 16. Neocomian; Comen, Istria, and Lesina, Dalmatia.

Pontosaurus Kramberger (*Hydrosaurus* Kornhuber *nec* Wagler). Neocomian; Lesina, Dalmatia. *Actaeosaurus* H. v. Meyer. ? *Mesoleptos* Cornalia. Neocomian; Comen, Istria. *Eidolosaurus* Nopcsa. Neocomian; Lesina.

Family 2. **Aigialosauridae.**[2]

Head large and neck short, with seven vertebrae. A few abdominal ribs. Fore limbs about as long as hind limbs. Lower Cretaceous.

This family includes semi-aquatic lizards, and seems to connect the *Dolichosauridae* with the *Pythonomorpha*.

Aigialosaurus Kramberger. Snout much attenuated. Seven cervical, twenty other presacral vertebrae. *A. dalmaticus* Kr. Neocomian; Lesina, Dalmatia.

Carsosaurus Kornhuber. Interclavicle T-shaped. Neocomian; Comen, Istria.

Opetiosaurus Kornhuber (Fig. 429). A movable articulation behind the middle of the mandibular ramus as in the *Pythonomorpha*. Type species about 1·5 m. long. Lesina.

The known Tertiary *Lacertilia* are very fragmentary, and belong for the most part to existing families. The earliest remains, from the Lower Eocene (Upper Landenian) of Belgium, belong to *Saniwa* Leidy, which is represented chiefly in the Middle Eocene (Bridger) of Wyoming. According to Gilmore,

[1] *Kornhuber, A.*, Über einen neuen fossilen Saurier aus Lesina. Abhandl. k. k. geol. Reichsanst. Wien, vol. v., p. 75, 1873.—*Meyer, H. von, Actaeosaurus Tommasinii.* Palaeontogr., vol. vii., p. 223, 1860.—*Nopcsa, F.*, Neues über Dolichosaurier. Beitr. Paläont. u. Geologie Österr.-Ungarns, vol. xxi., p. 50, 1908.—*Seeley, H. G.*, Small Lizard from the Neocomian Rocks of Comen, near Trieste [*Adriosaurus*]. Quart. Journ. Geol. Soc., vol. xxxvii., p. 52, 1881.

[2] *Cornalia, E.*, Cenni geologici sull' Istria. Giorn. R. Istit. Lombardo, etc., vol. iii., p. 35, 1851.—*Kornhuber, A.*, *Carsosaurus marchesettii.* Abhandl. k. k. geol. Reichsanst. Wien, vol. xvii., pt. 3, p. 1, 1893.—*Opetiosaurus bucchichi. Loc. cit.*, pt. 5, p. 1, 1901.—*Kramberger, C. Gorganovic, Aigialosaurus.* Schrift. Soc. hist.-nat. croatica, Agram, vol. vii., p. 74, 1892.

this genus is related to *Varanus*, but differs in having more numerous teeth, the postorbital and postfrontal separate, fewer cervical vertebrae bearing hypapophyses, and a vestigial zygosphene. In the Middle Eocene of Wyoming there are also *Anguidae* (*Glyptosaurus* Marsh, *Xestops* Cope, *Helodermoides* Douglass), *Iguanidae* (*Iguanavus* Marsh), and *Chamaeleontidae*. *Iguana* itself, now restricted to America, occurs in the European Tertiary. Fragmentary remains of other genera are found in the Eocene or Oligocene Phosphorites of Quercy, and Gypsum Beds of Apt, in France, among which may be mentioned the following: *Placosaurus* Gervais (*Necrodasypus* Filhol; *Loricotherium* Weigelt), apparently related to the existing N. American *Heloderma* Wiegm., *Proiguana* Filhol (Fig. 430), *Plestiodon* Filhol (Fig. 431), *Palaeovaranus* Filhol (Fig. 432), *Prochamaeleo* de Stefano, *Agama*, *Diploglossus*, and *Lacerta*. *Placosaurus* is also found in the Middle Eocene lignite of the Geiselthal, central Germany. Numerous remains also occur in the Oligocene (White River Beds) of western North America, representing *Amphisbaenidae* (*Rhineura* Cope, allied to L. Eocene *Ototriton* Loomis), *Helodermatidae*, and other families.

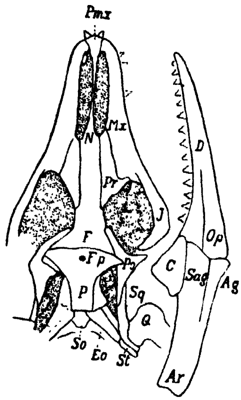


FIG. 429.

Opetiosaurus bucchichi Kornhuber. Skull with right ramus of mandible. Lower Cretaceous; Lesina. *Ag*, angular; *Ar*, articular; *C*, coronoid; *D*, dentary; *Eo*, exoccipital; *F*, frontal; *Fp*, pineal foramen; *J*, jugal; *L*, lachrymal; *Mx*, maxilla; *N*, nasal; *P*, parietal; *Pmx*, premaxilla; *Po*, postfrontal; *Pr*, prefrontal; *Q*, quadrate; *Sag*, surangular; *So*, supraoccipital; *Sq*, squamosal; *St*, supratemporal. $^1/_2$ nat. size (after Nopcsa).

The Miocene yields Lacertilian fragments identifiable with recent genera, especially in the freshwater beds of the Auvergne, France; the lignites of Rott, near Bonn; and the freshwater strata of Steinheim, Haslach, Günzburg, Sansan, and Colorado. Among Pliocene fossils there are vertebrae and other remains of *Varanus* from the Pontian Beds of Pikermi, Greece, and from the Siwalik Beds of India. In the Pleistocene of Queensland and other parts of Australia occurs the largest known lizard, probably 5 m. in

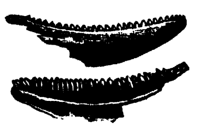


FIG. 430.

Proiguana sp. Inner and outer aspect of dentary. Phosphorite of Quercy. Nat. size.

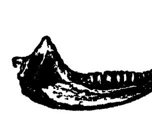


FIG. 431.

Plestiodon cadurcensis Filhol. Inner aspect of dentary. Phosphorite of Quercy. Nat. size.

FIG. 432.

Palaeovaranus cayluxi Filhol. Maxillary fragment. Phosphorite of Quercy. Nat. size.

length, *Megalania prisca* Owen.[1] This is known chiefly by vertebrae which much resemble those of *Varanus* but bear a slight zygosphene-zygantrum

[1] *Anderson, C.*, *Varanus* (*Megalania*) *priscus* (Owen). Rec. Australian Mus., vol. xvii., p. 311, 1930.—*De Vis, C. W.*, *Megalania* and its Allies. Proc. Roy. Soc. Queensland, vol. vi., p. 93, 1889.—*Etheridge, R.*, Occurrence of *Megalania* Owen in South Australia. Rep. Govern. Geologist S. Australia, 1894, p. 19.—*Fejérváry, G. J. de*, Fossil *Varanidae* and *Megalanidae*. Ann. Mus. Nat. Hungar., vol. xvi., p. 445, 1918.—*Owen, R.*, Gigantic Land-Lizard (*Megalania prisca* Owen) from Australia. Phil. Trans. Roy. Soc., 1859, p. 43. Also *loc. cit.*, 1880, p. 1037, and 1886, p. 327.—Large extinct Lizard [*Notiosaurus*] from Australian Pleistocene Deposit. *Loc. cit.*, vol. 175, p. 249, 1885.—*Woodward, A. S.*, Extinct Reptilian Genera *Megalania* Owen and *Meiolania* Owen. Ann. Mag. Nat. Hist. [6], vol. ii., p. 85, 1888.

articulation. A large jaw from the same formation and region is named *Notiosaurus* Owen.

Sub-Order 2. PYTHONOMORPHA.[1]

Large marine reptiles with elongate body and two pairs of paddle-shaped limbs. Skull lizard-like, elongate, depressed; upper temporal arch and pineal foramen present; premaxillae and nasals fused into a simple rostrum; quadrate large, perforate, and movably attached to squamosal and supratemporal; parietal unpaired and joined to the supraoccipital and prootics by decurved lateral processes. Mandibular rami united at the symphysis by ligament; a movable articulation behind the middle of each ramus. Teeth large and usually conical, fixed by tumid bases in shallow alveoli of the jaw-bones and pterygoids. Sclerotic ring present. Vertebrae procoelous; cervicals seven, mostly with hypapophyses. Sacrum wanting; sternum probably never ossified; interclavicle (episternum) sometimes present, but no clavicular arch. Limb bones short, but the digits lengthened by an increased number of phalanges, without claws.

The *vertebral column* comprises 115-130 or perhaps more procoelous vertebrae, and is sometimes divisible into cervical, dorsal, lumbar, and caudal regions. The distinction between dorsal and lumbar series is not very decided, however, except that the latter bear shorter ribs. The transverse processes are short and thick in the precaudal vertebrae for the attachment of single-headed ribs; in the caudals they are flattened and elongated but without ribs, and they disappear at about the middle of the tail. The neural

[1] *Baur, G.*, Morphology of Skull of *Mosasauridae*. Journ. Morphol., vol. vii., p. 1, 1892.—*Capps, S. R.*, Girdles and Hind Limb of *Holosaurus abruptus* Marsh. Journ. Geol., vol. xv., p. 350, 1907.—*Cope, E. D.*, Reptilian Orders of *Pythonomorpha* and *Streptosauria*. Proc. Boston Soc. Nat. Hist., vol. xii., p. 250, 1869.—Vertebrata of Cretaceous Formations of the West. Rep. U.S. Geol. Surv. Territ., vol. ii., p. 113, etc., 1875.—Professor Owen on *Pythonomorpha*. Bull. U.S. Geol. Surv. Territ., vol. iv., p. 299, 1878.—*Dollo, L.*, Note sur l'ostéologie des Mosasauridae. Bull. Mus. Roy. Hist. Nat. Belg., vol. i., p. 55, 1882.—Première Note sur le Hainosaure. *Loc. cit.*, vol. iv., p. 125, 1885.—Sur le crâne des Mosasauriens. Bull. Scient. France Belg., vol. xix., p. 1, 1888.—Mosasauriens de Mesvin. Bull. Soc. Belge Géol., etc., vol. iii., Mém., p. 271, 1889.—Mosasauriens de Maestricht. *Loc. cit.*, vol. iv., p. 151, 1890.—Nouvelle Note sur l'ostéologie des Mosasauriens. *Loc. cit.*, vol. vi., Mém., p. 219, 1892—Les Ancêtres des Mosasauriens. Bull. Scient. France Belg., vol. xxxviii., p. 1, 1903.—Les Mosasauriens de la Belgique. Bull. Soc. Belge Géol., etc., vol. xviii., Mém., p. 207, 1904.—L'Origine des Mosasauriens. *Loc. cit.*, p. 217, 1904.—Un nouvel opercule tympanique de *Plioplatecarpus*. *Loc. cit.*, vol. xix., Mém., p. 125, 1905.—*Globidens alabamaensis* et les Mosasauriens de la Belgique en général. Archives de Biologie (Liége), vol. xxxiv., p. 167, 1924.—*Gaudry, A.*, Les Pythonomorphes de France. Mém. Soc. Géol. France, Paléont. no. 10, 1892.—*Huene, F. von*, Ein ganzes *Tylosaurus*-Skelett. Geol. u. Palaeont. Abhandl., n.s., vol. viii., p. 297, 1910.—*Platecarpus*. Neues Jahrb. f. Min., etc., 1911, vol. ii., p. 48.—*Loomis, F. B.*, New Mosasaur from the Ft. Pierre. Amer. Journ. Sci. [4], vol. xxxix., p. 555, 1915.—*Marsh, O. C.*, *Edestosaurus*, etc. Amer. Journ. Sci. [3], vol. i., p. 448, 1871.—Skull and Limbs in Mosasauroid Reptiles. *Loc. cit.*, vol. iii., p. 448, 1872.—New Characters of Mosasauroid Reptiles. *Loc. cit.*, vol. xix., p. 83, 1880.—*Merriam, J. C.*, Pythonomorphen der Kansas Kreide. Palaeontogr., vol. xli., p. 1, 1894.—*Nopcsa, F.*, Origin of Mosasaurs. Geol. Mag. [4], vol. x., p. 119, 1903.—*Osborn, H. F.*, Complete Mosasaur Skeleton. Mem. Amer. Mus. Nat. Hist., vol. i., p. 167, 1899.—Cervical Region of Mosasaurs, etc. Amer. Nat., vol. xxxiv., p. 1, 1900.—*Owen, R.*, Rank and Affinities of Mosasauridae. Quart. Journ. Geol. Soc., vol. xxxiii., p. 682, 1877; also vol. xxxiv., p. 748, 1878.—*Pompeckj, J. F.*, Mosasaurier-Resten im Ober-Senon von Haldem. 3. Jahresb. Niedersächs. Geol. Vereins, p. 122, 1910.—*Thevenin, A.*, Mosasauriens de la Craie grise, etc. Bull. Soc. Géol. France [3], vol. xxiv., p. 900, 1896.—*Williston, S. W.*, Kansas Mosasaurs. Univ. Geol. Surv. Kansas, vol. iv. (Paleont. pt. i.), p. 81, 1898.—Relationships and Habits of Mosasaurs. Journ. Geol., vol. xii., p. 43, 1904.—*Wiman, C.*, Reptiles from the Niobrara Group in Kansas. Bull. Geol. Inst. Upsala, vol. xviii., p. 9, 1920.—*Yakowlew, N.*, Mosasaurien dans le Crétacé supérieur du sud de la Russie. Bull. Comité Géol. St. Pétersb., vol. xx., p. 507, 1901.—Les Mosasauriens. *Loc. cit.*, vol. xxiv., p. 135, 1906.

arches are always coössified with their centra; the neural spines are of moderate length, but sometimes notably elongated in the posterior region of the tail. The zygapophyses are strong in the cervical and anterior thoracic region, but become weaker and finally disappear in the tail. Y-shaped haemapophyses or chevron bones are present in all the caudals with the exception of the first five or more, to which the name "pygals" has been given; each chevron articulates only with its own centrum. The atlas is composed of a wedge-shaped intercentrum (hypocentrum) below, and two lateral pieces or neurapophyses, as in lizards, its centrum being represented by the odontoid process of the axis. A wedge-shaped intercentrum occurs between the atlantal intercentrum and the axis. The axis and five following cervicals bear each a more or less stout exogenous hypa-

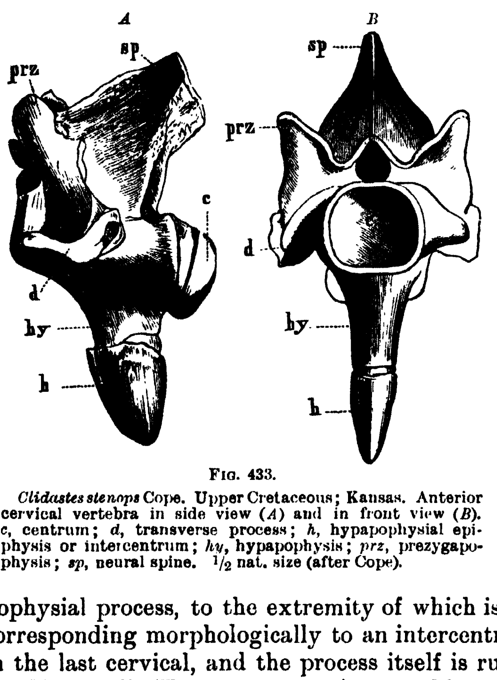


FIG. 433.

Clidastes stenops Cope. Upper Cretaceous; Kansas. Anterior cervical vertebra in side view (*A*) and in front view (*B*). *c*, centrum; *d*, transverse process; *h*, hypapophysial epiphysis or intercentrum; *hy*, hypapophysis; *prz*, prezygapophysis; *sp*, neural spine. 1/2 nat. size (after Cope).

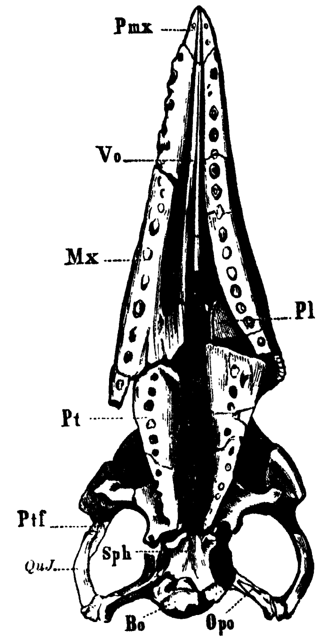


FIG. 434.

Clidastes propython Cope. Palatal aspect of skull, partly restored. Upper Cretaceous; Kansas. *Bo*, basioccipital; *Mx*, maxilla; *Pl*, palatine; *Pmx*, premaxilla; *Pt*, pterygoid; *Ptf*, postorbitofrontal; *Opo*, supratemporal; *QuJ*, squamosal; *Sph*, basisphenoid; *Vo*, vomer.

pophysial process, to the extremity of which is attached a small, free epiphysis, corresponding morphologically to an intercentrum (Fig. 433). This is wanting in the last cervical, and the process itself is rudimentary.

The *skull* (Figs. 434, 435) resembles that of *Varanus* more nearly than that of other living reptiles. The parietals, frontals, and premaxillae are all unpaired, as are also the nasals, which are fused with the premaxillae. The supratemporal vacuity is bounded externally by the squamosal and postorbital, which form a narrow arch. The supratemporal is intercalated between the exoccipital (= paroccipital, Baur) and the squamosal, and sends a slender process inwards between the exoccipital and proötic, extending nearly as far as the brain cavity. The suture between the postorbital and postfrontal is often obliterated. Supraciliary plates have not been observed, and are often functionally replaced by the horizontally

expanded prefrontals. The jugal unites with a descending process of the postfrontal, and these two bones with the prefrontal completely enclose the orbit. There is a complete parietal arch formed by a slender process of the parietal uniting with a process of the squamosal.

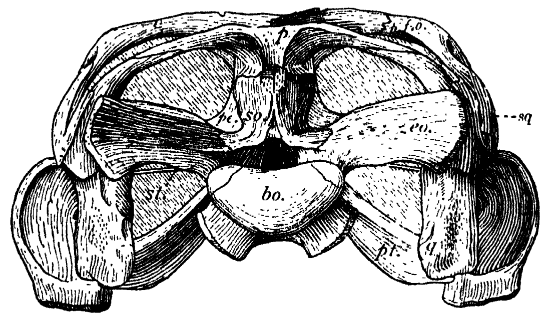


FIG. 435.

Platecarpus coryphaeus Cope. Posterior aspect of skull. Upper Cretaceous; Kansas. *bo*, basioccipital; *eo*, exoccipital; *p*, parietal; *pe*, prootic; *pfo*, postorbito-frontal; *pt*, pterygoid; *q*, quadrate; *so*, supraoccipital; *sq*, squamosal; *st*, stapes. 1/4 nat. size (after Williston).

The quadrate (Figs. 436, 437) is relatively large, and movably articulated with the squamosal and supratemporal. Its antero-superior margin is dilated into a broad thin plate, and its posterior margin is notched or perforated for the auditory meatus. This opening is either partially or completely enclosed posteriorly by the stout suprastapedial process which is especially characteristic of the Mosasaur quadrate. On the concave inner side of the quadrate, near the upper part of the meatal notch, is a small pit for the lodgment of the outer end of the stapes. The quadrate exhibits wide variation in form and size among the different genera.

The transverse bone, or ectopterygoid, is always small, and joins the pterygoid and jugal only. A slender columella, or epipterygoid, is present

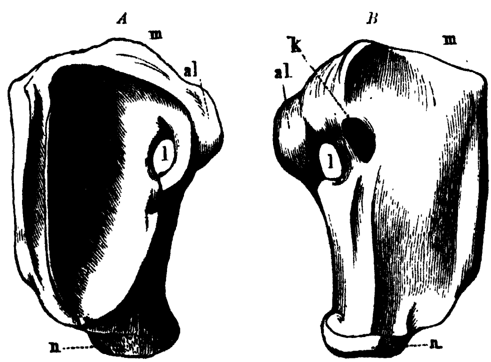


FIG. 436.

Mosasaurus camperi v. Meyer. Quadrate bone, outer (*A*) and inner (*B*) aspect. Upper Cretaceous; Maastricht. *al*, suprastapedial process; *k*, stapedial pit; *l*, meatus; *m*, superior margin; *n*, inferior margin. 1/4 nat. size (after Owen).

FIG. 437.

Clidastes propython Cope. Quadrate bone, inner aspect. Lettering as in Fig. 436. 2/3 nat. size (after Cope).

in all cases. The mandibular rami were united at the symphysis by ligament. Somewhat behind the middle of each ramus, between the angular and splenial, and the dentary and surangular, there is a movable articulation permitting of a wide distension of the jaws.

A single series of large conical teeth (rarely short and tumid) occurs in both upper and lower jaws, those of the pterygoid being smaller than the rest. The crown often exhibits slight anterior and posterior carinae, and

may be bevelled into several longitudinal facets; the enamelled surface may be either smooth or delicately striated. All the teeth are fixed by tumid bony bases in shallow pits of the supporting bone. Successional teeth arise alongside those in function, and gradually displace them by pressure against the crown on the inner side.

The *pectoral arch* (Fig. 438) exhibits a rather large and flattened coracoid, the articular border of which is thickened and divided into two facets meeting at an obtuse angle, while the thin inner edge is rounded and often incised by a deep notch or emargination. There is a small coracoid foramen situated towards the articular border. Posteriorly the coracoids meet the sternum, which was probably never ossified, but composed of calcified cartilage, like the sternal ribs. The coracoids are separated from each other by a

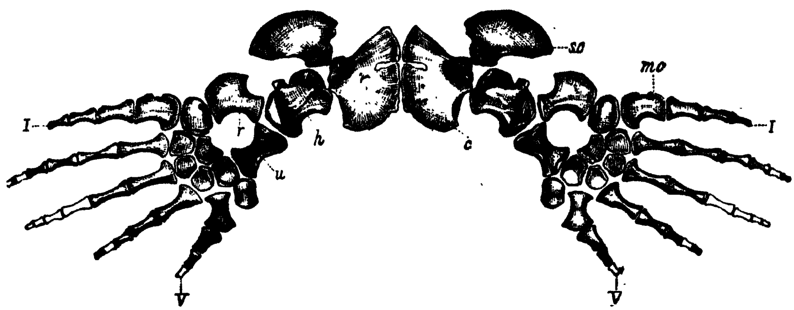


FIG. 438.

Clidastes velox Marsh sp. Pectoral arch, dorsal aspect. Upper Cretaceous; Kansas. *c*, coracoid; *h*, humerus; *mc*, metacarpus; *r*, radius; *sc*, scapula; *u*, ulna; *I-V*, digits. The coracoids are wrongly placed in contact in the median line; they should be separated to leave space for a cartilaginous extension and a sternum, as in the *Lacertilia*. $^1/_5$ nat. size (after Marsh).

broad epicoracoidal expanse of cartilage. The scapula is placed as in Rhynchocephalians; a slender rod-shaped interclavicle (episternum) is present, but clavicles are absent. The humerus is short and stout, its articular ends expanded, and the distal end with two facets for the bones of the second segment. Of the latter the radius is distally expanded. The carpals vary in number from seven (arranged in two rows) in *Clidastes* and *Mosasaurus*, to one or two rudimentary ossicles in *Tylosaurus*. There are five metacarpals, differing in shape among the various genera, and supporting a variable number of phalanges; these last being comparatively few in *Clidastes* and *Mosasaurus*, and as many as eleven or twelve in the paddles of *Tylosaurus*. None of the digits are clawed.

The *pelvic arch* (Fig. 439) is more weakly developed than the pectoral. The ilium is a slender rod-shaped bone, its superior end free or loosely attached to the single vertebra which functions as a sacrum. The pubes probably do not meet in a ventral symphysis, but the ischia are joined along an extensive articular surface. The bones of the hind limb resemble those of the fore limb, but are more slender, and somewhat smaller. There are probably never more than three tarsals, and sometimes only one. Four or five digits are developed, with a variable number of phalanges.

The limbs of Pythonomorphs, Ichthyosaurs, and Cetaceans furnish an excellent illustration of the influence of environment in producing analogous structures among widely divergent groups. As a result of their complete

adaptation for an aquatic existence, Mosasaurs, Ichthyosaurs, and whales have developed a very similar form of body.

The Pythonomorphs had a wide distribution, their remains being known from the Upper Cretaceous of Europe, Palestine, Morocco, Nigeria, Timor, South Africa, North and South America, and New Zealand. It is curious that young individuals do not appear to have been hitherto discovered. As remarked by Williston, it is likely that these reptiles were oviparous, and they may have laid their eggs in estuaries and bays of which the sediments have not been preserved.

The Pythonomorphs were covered externally with scales very similar in size and structure to those of *Varanus*. These scales have been found

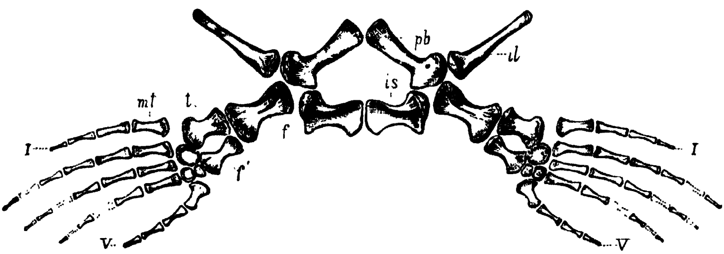


FIG. 439.

Platecarpus simus Marsh sp. Pelvic arch and paddles. Upper Cretaceous; Kansas. *f*, femur; *f'*, fibula; *il*, ilium; *is*, ischium; *mt*, metatarsus; *pb*, pubis; *t*, tibia; *I-V*, digits. $^1/_{12}$ nat. size (after Marsh).

impressed on the bones of the skull, indicating the absence of horny plates. There were no dermal ossifications of any kind. As pointed out by Dollo,[1] the Pythonomorphs with stout conical teeth were probably predaceous and fed on fishes or even other reptiles, while those with slender conical teeth doubtless fed on soft Cephalopods. The few with crushing teeth (*Globidens*) seem to have eaten Echinoderms. Small or medium-sized fishes have been observed in the fossilised stomach-contents in several instances.

The earliest discovered cranium, found in the Maastricht Chalk in 1780, was mistaken for that of a Cetacean or Crocodilian until Camper and Cuvier demonstrated its remarkable similarity to the skull of *Varanus*. Owen united Mosasaurs with lizards under the designation of *Lacertilia natantia*. The name *Pythonomorpha* was proposed in 1869 by Cope, who regarded the group as intermediate between snakes and lizards.

Family 1. **Mosasauridae**.

Trunk elongated, tail much dilated distally. Premaxillae forming a short and obtusely conical rostrum. Prefrontals more or less dilated into a horizontal plate posteriorly. Quadrate with moderate-sized suprastapedial process. Coronoid large, articulating with the splenial on the inner side. Zygosphenes rudimentary or functional; chevrons fused with their centra. Humerus with strong radial process at distal end. Hind limb tetradactyl. Carpus and tarsus completely ossified; not more than six phalanges in any of the digits. Upper Cretaceous.

Surface-swimming Mosasaurs.

[1] *Dollo, L., Globidens fraasi . . .* et l'Ethologie de la Nutrition chez les Mosasauriens. Archives de Biologie (Liège), vol. xxviii., p. 609, 1913.

Clidastes Cope (*Edestosaurus* Marsh) (Figs. 433-434, 437-438, 440). Skull 40 to 70 cm. long; slender, tapering, depressed. Teeth faceted on outer side, and smooth on the inner or on both faces. Dentary with about seventeen teeth, maxilla fifteen, pterygoid twelve to fifteen. Zygosphenes functional; chevrons long. Neural spines elevated in posterior half of the tail, suggesting presence of a caudal fin. Upper Cretaceous; Kansas, Alabama, and New Jersey, U.S.A.

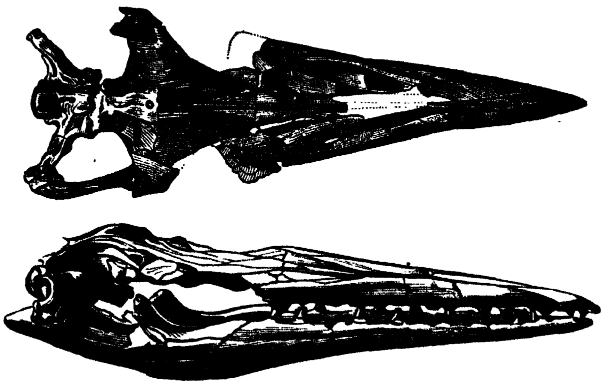


FIG. 440.
Clidastes propython Cope. Skull and mandible, upper and lateral aspects. Upper Cretaceous; Uniontown, Alabama. 1/5 nat. size (after Cope).

Mosasaurus Conyb.[1] (*Leiodon* Owen; *Pterycollasaurus* Dollo) (Figs. 436, 441). Skull attaining a length of 1·2 m.; total length about 12 m. Distinguished from *Clidastes* chiefly by the usual absence of a zygosphene-zygantrum articulation. There are more than 130 vertebrae in the column, of which 46 are precaudal. The massive upper jaws are armed with about fourteen powerful teeth on either side, and the pterygoids support about eight smaller teeth, all with anterior and posterior carinae. Upper Cretaceous; Holland, England, Belgium, France, Northern Germany, Northern Italy, Morocco, Nigeria, and the United States.

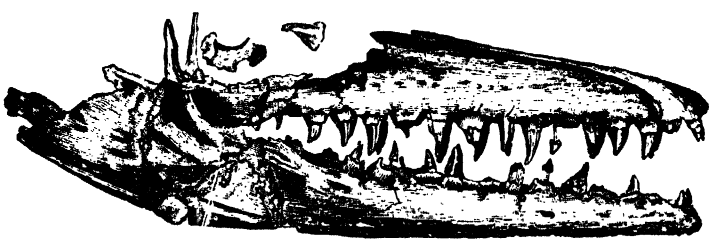


FIG. 441.
Mosasaurus camperi v. Meyer. Jaws, side view. Upper Cretaceous; Maastricht. 1/12 nat. size (after Dollo).

Family 2. Platecarpidae.

Trunk short, tail proportionately long. Premaxillae short, very obtuse, and projecting but little in front of the teeth. Quadrate with a long suprastapedial process. Vertebrae with rudimentary zygosphenes. Interclavicle probably present in all forms. Hind limb functionally pentadactyl. Carpus and tarsus imperfectly ossified. Upper Cretaceous.

[1] *Cuvier, G.*, Sur le grand animal fossil de la Craie de Maestricht. Ann. Mus. Hist. Nat. Paris, vol. xii., p. 145, 1808.

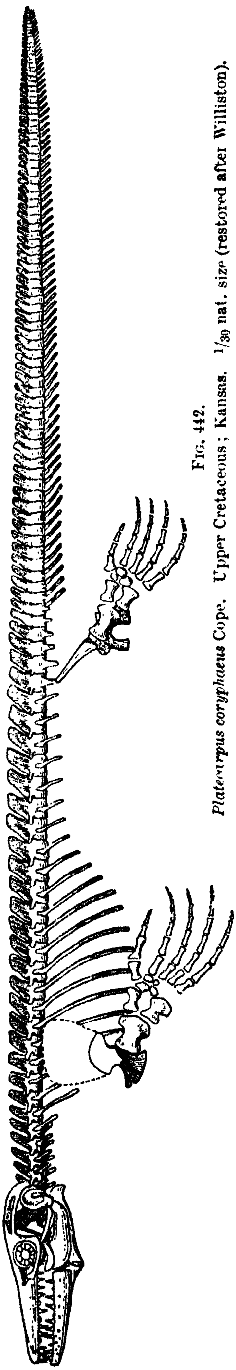


Fig. 442.
Platecarpus coryphaeus Cope. Upper Cretaceous; Kansas. 1/30 nat. size (restored after Williston).

Platecarpus Cope (*Lestosaurus* Marsh; ? *Holcodus* Gibbes) (Figs. 435, 439, 442, 443). Total length about 5 m., of which the skull forms one-eighth. Superior surface of parietal small, triangular, not reaching beyond the middle of the bone; large oval pineal foramen at its anterior border. External nares much dilated anteriorly. Quadrate with prominent suprastapedial process extending below the middle of the bone; opening for the auditory meatus large, not entirely enclosed. Teeth slender and recurved, faceted on the outer side, striate on the inner; maxilla with

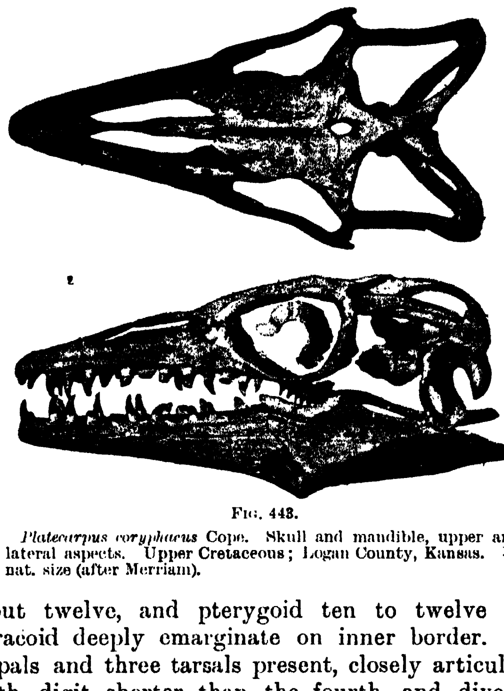


Fig. 443.
Platecarpus coryphaeus Cope. Skull and mandible, upper and lateral aspects. Upper Cretaceous; Logan County, Kansas. 1/7 nat. size (after Merriam).

about twelve, and pterygoid ten to twelve teeth. Coracoid deeply emarginate on inner border. Four carpals and three tarsals present, closely articulating. Fifth digit shorter than the fourth, and divergent. Chevron bones large, loosely articulated. Abundant and represented by numerous species in the Upper Cretaceous of Kansas, Wyoming, Colorado, Texas, North Dakota, and France.

Holosaurus Marsh. Very similar to the preceding, except that the coracoids are not emarginate; there are no zygosphenes in the type specimen. Kansas.

Plioplatecarpus Dollo (*Oterognathus*, *Phosphorosaurus* Dollo). Similar to *Platecarpus*, but with smaller chevron bones. Mandible slender, coronoid rudimentary. Teeth long and slender, faceted, and striate. Tympanic membrane calcified. Danian of Maastricht, and Upper Senonian of Belgium.

Prognathosaurus Dollo. Skull about 60 cm. long. Pterygoids nearly as large as the maxillae, and with very powerful teeth. The large suprastapedial process of the quadrate coössifies with the infrastapedial process, and encloses an oval foramen. A wide canal present in lower part of the basioccipital. Mandible strong, upper edge concave, coronoid process prominent. Coracoid non-emarginate. Chevrons loosely articulated. Upper Senonian (Phosphatic Chalk); Belgium.

Brachysaurus Williston (*Ancylocentrum* K. P. Schmidt). Frontal large and broad; no median basioccipital canal. Suprastapedial process of quadrate coössified with the infrastapedial. No zygosphenes; chevrons fused with their centra. Possibly identical with preceding genus. Ft. Pierre Cretaceous; South Dakota.

Sironectes Cope. Upper Cretaceous; Kansas.

Baptosaurus Marsh. Upper Cretaceous; New Jersey and Kansas.

Dollosaurus Yakowlew. Senonian; Russia.

Taniwhasaurus Hector. Cretaceous; New Zealand.

Family 3. **Tylosauridae.**

Trunk short, tail proportionately long. Premaxillae produced into a long rostrum in advance of the teeth; quadrate with short suprastapedial process. Vertebrae without, or with very rudimentary zygosphenes. Carpus and tarsus almost wholly unossified; phalanges numerous. Hind limb functionally pentadactyl. Upper Cretaceous.

Very large Mosasaurs with bones often imperfectly ossified, adapted for diving to great depths.

Tylosaurus Marsh (*Liodon* Cope; *Macrosaurus* Owen; *Rhinosaurus* Marsh). Skull 0·7 to over 1 m. long. Superior surface of parietal smooth and produced to the posterior margin in the median line, with nearly parallel sides; foramen at its anterior margin. Postfrontal and prefrontal meeting on the superior border of the orbit; quadrate stout, with very short suprastapedial process, and tympanic membrane replaced by calcified cartilage; maxilla with about thirteen large teeth. Chevrons loosely articulated; no zygosphenes. One or two carpal and tarsal bones present, not articulating with adjacent elements. Coracoid not emarginate; limbs about equally developed; phalanges numerous; fifth digit elongate. Niobrara Group; Kansas, New Mexico, and Texas. *T. proriger*, *T. dyspelor* Cope. Also South Africa.[1]

Hainosaurus Dollo. Skull upwards of 1·5 m. long. Frontal broad; prefrontal and postfrontal meeting over the orbit; teeth of unequal size. Haemapophyses loosely articulated; cervicals with small zygosphenes. Carpals reduced in number; phalanges fewer than in *Tylosaurus*, and paddles relatively larger. Upper Cretaceous; Belgium.

Family 4. **Globidentidae.**[2]

Skull short and massive. Teeth with low blunt and tumid crown. Vertebrae with small zygosphenes. Upper Cretaceous.

[1] *Broom, R.*, Tylosaurus from Upper Cretaceous of Pondoland. Ann. S. African Mus., vol. vii., p. 332, 1912.

[2] *Dollo, L.*, *Globidens fraasi.* Archiv. Biologie (Liége), vol. xxviii., p. 609, 1913.—*Globidens alabamaensis. Loc. cit.*, vol. xxxiv., p. 167, 1924.—*Gilmore, C. W.*, New Mosasauroid Reptile from Cretaceous of Alabama. Proc. U.S. Nat. Mus., vol. 41, p. 479, 1912.

These are the only known Pythonomorphs with teeth adapted for crushing hard food.

Globidens Gilmore. Known only by fragments. Teeth with finely wrinkled enamel. *G. alabamaensis* Gilm., with maxilla at least 25 cm. in length. Selma Chalk; Alabama. *G. fraasi* Dollo. Maastricht, Holland. *G. belgicus* A. S. Woodward. Ciply, Belgium.

? *Coniasaurus* Owen. Jaws and vertebrae from English Chalk.

Sub-Order 3. OPHIDIA. Snakes.[1]

Body elongated, without limbs, covered with horny epidermal scales. Temporal arches of skull absent; columella (epipterygoid) absent; quadrate movable. Parietal unpaired, without pineal foramen, the sides extended downward and fused with the proötic, alisphenoid and orbitosphenoid. Anterior portion of brain case completely ossified. Maxillae, palatines, and pterygoids freely movable. Premaxillae much reduced; mandibular symphysis ligamentous. Vertebrae procoelous, with zygosphene-zygantrum articulation, and the anterior centra with strong simple hypapophyses.

Snakes are chiefly conspicuous for the absence of limbs. The body is greatly elongated, and the number of vertebrae very considerable, sometimes exceeding 500. The centra are concave in front and convex behind, the connection being by free ball-and-socket joints; and their articulation is further strengthened by zygapophyses and a zygosphene-zygantrum arrangement. The neural arches are thoroughly coössified with their centra. Simple hypapophyses are developed by the anterior vertebrae sometimes as far as the thirtieth, and the transverse processes are short and tumid (Fig. 444). Ribs are almost always present in the trunk region, beginning with the third vertebra; and being freely articulated by a single head, are able to assist in propelling the body. They are long, curved, and frequently hollow; in the caudal region they are replaced by elongate transverse processes. Haemapophyses are wanting among snakes, and in their stead occur stout descending branches of the transverse processes (Fig. 445).

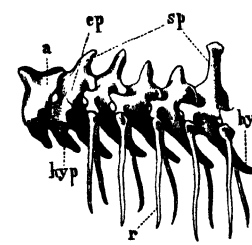


FIG. 444.

Python bivittatus Schn. Recent; Sumatra. Anterior cervical vertebrae. *a*, atlas; *ep*, axis; *hyp*, hypapophysis; *r*, rib; *sp*, neural spine. Nat. size (after d'Alton).

The *cranium* (Fig. 446) differs from that of lizards in the constant absence

[1] *Andrews, C. W.*, Ophidian Vertebrae from Nigeria. Bull. Geol. Surv. Nigeria, no. 7, 1924.—*Bolkay, St. J.*, *Mesophis nopcsai* n.g., n.sp. Publication of Bosnia-Hercegovina State Museum, Sarajevo, vol. xxxvii., p. 125, 1925.—*Filhol, H.*, Ann. Sci. Géol., vol. viii., p. 270, 1887.—*Fischer, G.*, De serpentibus quibusdam fossilibus dissertatio. Bonn, 1857.—*Janensch, W.*, Über *Archaeophis*, etc. Beitr. Pal. u. Geol. Österr.-Ungarns, vol. xix., p. 1, 1906.—*Pterosphenus schweinfurthi* Andrews, und die Entwicklung der Palaeophiden. Archiv f. Biontologie, vol. i., p. 311, 1906.—*Kerr, J. G.*, *Bothrodon pridii*, an Extinct Serpent of Gigantic Dimensions. Proc. Roy. Soc. Edinb., vol. xlvi., p. 314, 1926.—*Leriche, M.*, *Palaeophis*. Bull. Soc. Belge Géol., vol. xxxvi., p. 21, 1926.—*Lucas, F. A.*, New Snake [*Pterosphenus schucherti*] from the Eocene of Alabama. Proc. U.S. Nat. Mus., vol. xxi., p. 637, 1899.—*Meyer, H. von*, *Coluber atavus* aus dem Siebengebirge. Palaeontogr., vol. vii., p. 232, 1860.—*Nopcsa, F.*, *Eidolosaurus* und *Pachyophis*. Palaeontogr., vol. lxv., p. 118, 1923.—Symoliophis-Reste. Abh. Bayer. Akad. Wiss., math.-nat. Abt., vol. xxx., Abh. 4, 1925.—*Rochebrune, A. T. de*, Révision des Ophidiens fossiles. Nouv. Arch. Musée d'Hist. Nat. Paris [2], vol. iii., p. 271, 1880.—*Roemer, F.*, Über *Python euboeicus*. Zeitschr. Deutsch. Geol. Ges., vol. xxii., 1870.—*Swinton, W. E.*, *Daunophis langi*, gen. et sp. nov. Ann. Mag. Nat. Hist. [9], vol. xvii., p. 342, 1926.—*Woodward, A. S.*, An extinct Ophidian, *Dinilysia patagonica*, gen. et sp. nov. Proc. Zool. Soc., 1901, p. 176.

of both temporal arches; complete ossification of the anterior part of the brain case; reduction of the premaxillae; absence of an epipterygoid; strong development of the ectopterygoid, which joins the maxillary and palato-pterygoid arches; and movable connection between not only all of the last-named bones, but between the squamosal and occipital region, and between the rami of the lower jaw. The brain cavity is very long, and its lateral walls as far as the middle portion are formed by descending processes of the parietal and frontal. The exoccipital and opisthotic are fused, and the maxilla is often much reduced. All the cranial bones are dense and ivory-like, and united by smooth sutures.

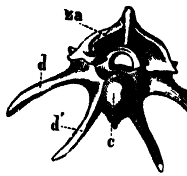


FIG. 445.

Python bivittatus Schn. Caudal vertebra, posterior aspect. *c*, centrum; *d*, *d'*, transverse process and its descending branch; *za*, zygantrum.

Slender, conical, recurved, acrodont teeth are usually present on the maxillae, premaxillae, pterygoids, palatines, and dentary bones. Occasionally they are wanting on the palatines (*Uropeltidae*), and often also on the rudimentary premaxillae. In the venomous snakes some of the maxillary teeth are hollow and traversed by a canal or groove ending in a slit-like opening at the end of the tooth. The canal is connected with the duct of a poison gland, and through it the secretion of the latter is forced when the animal strikes. Some of the non-poisonous snakes also have grooved teeth.

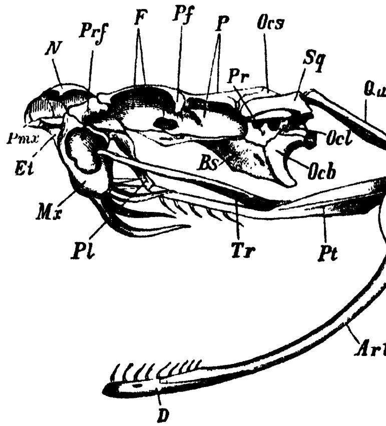


FIG. 446.

Crotalus horridus Linn. Recent; South America. *Art*, articular; *Bs*, basisphenoid; *D*, dentary; *Et*, ethmoid; *F*, frontal; *Mx*, maxilla; *N*, nasal; *Ocb*, basioccipital; *Ocl*, exoccipital; *Ocs*, supraoccipital; *P*, parietal; *Pf*, postfrontal; *Pl*, palatine; *Pmx*, premaxilla; *Pr*, proötic; *Prf*, prefrontal; *Pt*, pterygoid; *Qu*, quadrate; *Sq*, squamosal; *Tr*, transverse (ectopterygoid). Nat. size (after Claus).

Locomotion among snakes is accomplished by the lateral movements of the vertebral column, assisted by the ribs, the latter being alternately pushed forward and the epidermal scales drawn after them.

The existing *Ophidia* are distributed principally in the warmer regions, only the smaller forms extending into the temperate zone. By far the greater number are terrestrial, although some are amphibious, and a few are exclusively marine. Fossil remains are so rare and usually so fragmentary that the extinct *Ophidia* are only imperfectly known, and the systematic position of many of them is uncertain. The earliest specimens are from the Lower Cretaceous of Europe, but they cannot always be clearly distinguished from the remains of *Dolichosauridae*.

The oldest known *Ophidia*, as represented by *Pachyophis* Nopcsa, from the Neocomian of Hercegovina, belong to an ancestral or primitive group, the *Cholophidia* or *Cholophidae* of Nopcsa, which seem to have had the jaws comparatively rigid, the zygosphene small, and the ribs not yet completely adapted for the peculiar mode of progression characterising the typical snakes. They probably lived in the sea. *P. woodwardi* Nopcsa is about 40 cm. long,

with approximately 180 vertebrae, of which the 46 cervicals are elongated. The anterior ribs are much thickened; the tail is unusually short. *Mesophis* Bolkay, apparently with blunter skull and more laterally compressed trunk, is from the same formation and locality. Isolated vertebrae showing pachyostosis from the Cenomanian of Charente, France, of Pendão, Portugal, and of Egypt, are named *Symoliophis* Sauvage.

Some large sea snakes of the extinct family *Palaeophidae* are known only by vertebrae and ribs from the Eocene of western Europe, Africa, and southern North America. The ribs agree with those of *Pachyophis* in lacking the prominence (*tuber costae*) which usually occurs in the ribs of snakes on one side of the proximal articulation. The vertebrae have a high neural spine, a prominence above each postzygapophysis, and usually a hypapophysis both in front and behind. *Palaeophis* Owen, from Lower and Middle Eocene of England and Belgium, also Nigeria. *Titanophis* Marsh (*Dinophis* Marsh *nec* Hallowell) from Eocene, New Jersey, U.S.A., nearly similar. *Pterosphenus* Lucas (*Moeriophis* Andrews) from Upper Eocene, Alabama, U.S.A., and top of Middle Eocene, Fayum, Egypt, in both localities with *Zeuglodon.*

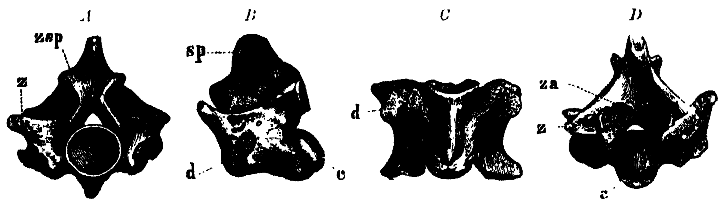


FIG. 447.

Palaeopython cadurcensis Filhol sp. Phosphorite of Quercy, France. *A*, Anterior; *B*, Lateral; *C*, Inferior; *D*, Posterior aspect of vertebra. *c*, centrum; *d*, transverse process with costal tubercle; *sp*, neural spine; *z*, zygapophysis; *za*, zygantrum; *zsp*, zygosphene. Nat. size.

Another sea snake, *Archaeophis proavus* Massalongo, is well preserved in the Upper Eocene of Monte Bolca, near Verona. According to Janensch it has about 565 vertebrae, and there are 450 pairs of ribs which do not show any *tuber costae*.

Several genera apparently of *Boidae* (*Protagras* Cope; *Boavus*, *Lithophis*, and *Lestophis* Marsh) have been described from the Eocene of Wyoming and New Mexico. Among the Oligocene *Boidae* of France, Switzerland, and England may be mentioned *Palaeopython* (Fig. 447) and *Scytalophis* Rochebrune, and *Paleryx* Owen; of Colorado, U.S.A., *Aphelophis* and *Calamagras* Cope.

One of the best preserved Miocene serpents is *Heteropython euboeicus* Roemer sp. from Kumi, on the island of Euboea. Representatives of the *Colubridae* (*Elaphis* Aldr.; *Coluber* Linn.) and *Erycidae* (*Scaphophis* Roch.) have been described from the freshwater Miocene of Oeningen, Steinheim, Günzburg, Haeder, Weissenau, Ulm, Sansan, Touraine, and other localities, as well as from the lignites of Rott, near Bonn. The earliest known poisonous snake is *Provipera* Kinkelin, from the Miocene of Mosbach-Biebrich. A species of *Bitis* Gray is recorded by Piveteau from the Upper Miocene (Pontian) of Libros, Teruel, Spain; and the so-called *Coluber kargii* H. von Meyer, from the Upper Miocene of Oeningen, Baden, also seems to belong to this genus. *Erycidae* and *Crotalidae* are known from the Miocene of Colorado and Oregon. *Daunophis* Swinton, a python. Upper Tertiary; South Burma.

Nearly all known Pleistocene remains are identifiable with existing genera,

but one unusually large poison fang found in a deposit of silt in the Gran Chaco, Paraguay, seems to belong to an extinct form. It is strongly curved, and measures nearly 6·5 cm. along the outside of the curve (*Bothrodon pridii* Graham Kerr).

Dinilysia A. S. Woodward, found with Dinosaurs and Mesosuchian Crocodiles in an Upper Cretaceous or Lower Tertiary formation in Neuquen, Argentina, S. America, is known by the skull and part of the vertebral column, representing a snake about 2 m. long. It seems to be related to the burrowing snakes of the family of *Ilysiidae* now existing in South America and southern Asia.

Gigantophis Andrews is a large python, not less than 9 m. in length, known by vertebrae from the Middle Eocene of the Fayum, Egypt.

Order 11. THECODONTIA.

As Rhynchocephalia, *but teeth on margin of jaw with a hollow base and vertical successor, each loosely implanted in a deep socket; teeth on palate rudimentary or absent; and at least some dorsal ribs double-headed. Dermal armour usually well developed.*

This is a generalised group from which both the *Crocodilia* and the *Dinosauria* may have been derived.

Sub-Order 1. EOSUCHIA.

Snout short, with paired external narial opening; no antorbital vacuity; a large pineal foramen; a tabular (or supratemporal) bone present; a vacuity in mandibular ramus. Intercentra throughout vertebral column.

Family 1. Younginidae.[1]

Orbit very large; snout slender and laterally compressed. Pubis and ischium plate-like, with a rhombic median pubo-ischiadic vacuity perhaps occupied by cartilage, and a pair of vacuities laterally. Humerus expanded distally, with entepicondylar foramen; hind limb slender. Permian and Triassic.

Youngina Broom. Skull rugose and pitted. Antorbital part occupying half total length of skull; lateral temporal much larger than superior temporal vacuity; small teeth on vomer, palatine, and pterygoid. A pair of ossified sternal bones. *Y. capensis* Broom, with skull 6 cm. long. Upper Permian (*Cistecephalus* Zone); Graaff Reinet District, S. Africa.

Paliguana Broom. Quadrato-jugal and jugal arch probably incomplete. Triassic (*Procolophon* Zone); Donnybrook, S. Africa.

Palaeagama Broom. Between *Youngina* and *Paliguana*. Fifth metatarsal short. *Cistecephalus* Zone; Kinira, Pondoland.

Saurosternum Huxley (*Batrachosaurus* Owen); *Heleosaurus*, *Heleophilus* Broom; *Noteosuchus* Broom (*Eosuchus* Watson *nec* Dollo). Permian; S. Africa.

? *Broomia* Watson. *Tapinocephalus* Zone; Beaufort West District, S. Africa.

[1] *Broom, R.*, New Thecodont Reptile [*Youngina*]. Proc. Zool. Soc., 1914, p. 1072.—Nearly complete Skeleton of a new Eosuchian Reptile (*Palaeagama vielhaueri* gen. et sp. nov.). *Loc. cit.*, 1926, p. 487.—*Huene, F. von*, Bibliographic references, etc. Palaeont. Hungarica, vol. ii., p. 67, 1926.—*Watson, D. M. S.*, *Eosuchus colletti.* Rec. Albany Mus., vol. ii., p. 298, 1912.—*Broomia perplexa.* Proc. Zool. Soc., 1914, p. 995 (also *Broom, R., loc. cit.*, 1921, p. 150).

Family 2. **Tangasauridae.**[1]

Aquatic Eosuchia *with short neck and body, long tail. Minute teeth on palate. Vertebrae pierced by notochord; strong neural spines. Humerus expanded at distal end, with entepicondylar foramen. Pubis and ischium plate-like, separated only by a rhombic median pubo-ischiadic vacuity, perhaps occupied by cartilage. Hind limb longer than fore limb. Abdominal ribs present.* Permian.

Tangasaurus Haughton. Head triangular. Coracoid elongated, with foramen; interclavicle with rhombic expansion anteriorly. Sternal plates paired in young, united in adult. Femur sigmoidally bent. Phalangeal formula, 2, 3, 4, 5, 3 (4). *T. mennelli* Haughton, probably about 40 cm. long. Tanga, Tanganyika Territory; and Madagascar.

Hovasaurus Piveteau. Coracoid rounded, not elongated. Sternal plates paired. Body longer and limbs shorter than in *Tangasaurus*. Quartz pebbles abundant in stomach (gastroliths). *H. boulei* Piv. S. Madagascar.

Sub-Order 2. PELYCOSIMIA.[2]

Snout short; an antorbital vacuity; pineal foramen small or absent; no tabular (or supratemporal) bone; no vacuity in mandibular ramus. Probably cartilaginous intercentra.

Family 1. **Erythrosuchidae.**

Premaxillae short, and external narial openings lateral, near end of snout. Parietal region relatively short and broad. Triassic.

Erythrosuchus Broom. Marginal teeth very deep, laterally compressed, more or less serrated on edges. No teeth on palate. Small pineal foramen. All vertebrae very short. Tail long and stout, anterior chevrons long. *E. africanus* Broom, with skull nearly 1 m. long. Upper Triassic (*Cynognathus* Zone); S. Africa.

Chasmatosaurus Haughton. Teeth as in *Erythrosuchus*. A row of minute teeth on pterygoid. No pineal foramen. *C. vanhoepeni* Haughton, with skull about 40 cm. long. Lower Triassic (*Lystrosaurus* Zone); Harrismith, Orange Free State, S. Africa.

? *Acompsosaurus* Mehl. Pelvis from Triassic, New Mexico, U.S.A.

Sub-Order 3. PARASUCHIA.

Snout much elongated, formed by extended premaxillae, with paired external narial opening at base near orbits; an antorbital vacuity; pineal foramen usually absent; tabular and postparietal bones present on occiput, but usually fused with parietals and supraoccipital respectively; a vacuity in mandibular ramus. No vertebral intercentra except in atlas and axis. Coracoid notched in place of foramen. Bony dermal plates well developed dorsally, in part ventrally.

[1] *Haughton, S. H.*, Reptilian Remains from the Karroo Beds of East Africa. Quart. Journ. Geol. Soc., vol. lxxx., p. 1, 1924.—Karroo Reptilia from Madagascar. Trans. Roy. Soc. S. Africa, vol. xviii., p. 125, 1929.—*Piveteau, J.*, Ann. Paléont., vol. xv., p. 55, 1926.

[2] *Haughton, S. H.*, New Type of Thecodont from Middle Beaufort Beds [*Chasmatosaurus*]. Ann. Transvaal Mus., vol. xi., p. 93, 1924.—*Huene, F. von*, Über *Erythrosuchus*. Geol. u. Palaeont. Abhandl., n.s., vol. x., p. 1, 1911.

The *Parasuchia* were thus named by Huxley, who regarded them as ancestral crocodiles. Although they have no secondary bony palate, the internal nares open into an arched cavity in the roof of the mouth formed by the solid palate, and the nasal passage may perhaps have been extended a little backwards by soft parts. According to C. L. Camp, small funnel-shaped foramina, which are scattered over the expanded end of the snout and lower jaw in some forms, probably lodged tactile organs.

Family 1. **Belodontidae.**[1]

Upper temporal vacuity open. Head bones sculptured. Abdominal ribs in three longitudinal series. Triassic.

Mesorhinus Jaekel. Skull depressed and external narial openings further forward than the antorbital vacuities. A small pineal foramen. Teeth laterally compressed and spatulate. *M. fraasi* Jaekel, with skull about 50 cm. long. Lower Triassic (Middle Bunter); Bernburg, N. Germany.

Belodon H. von Meyer (*Lophoprosopus* Mehl; ? *Phytosaurus* Jaeger) (Figs. 448, 450). Skull at least as deep as wide, and rostrum with an irregular, vertical, longitudinal bony crest; external narial openings above antorbital vacuities; no pineal foramen; parieto-squamosal arch behind the superior temporal vacuity depressed. Anterior teeth round in section, posterior teeth laterally compressed with two sharp edges. A paired series of transversely elongated, slightly overlapping, large dorsal plates, each with a prominent boss near its inner margin; flanked by a series of smaller plates on each side. *B. kapffi* H. von Meyer (Figs. 448, 450), known by well-preserved skulls about 75 cm. in length, also most parts of skeleton. Upper Triassic (Keuper); Würtemberg. The name *Phytosaurus* was given by Jaeger to indeterminable sandstone casts of tooth-sockets which are probably Belodont, but not generically identifiable.

Machaeroprosopus Mehl (*Metarhinus* Jaekel *nec* Osborn; *Pseudopalatus* Mehl) (Fig. 449). Rostral crest less developed than in *Belodon*. The snout relatively longer and more slender in the young than in the adult. *M. validus* Mehl, with skull about 1 m. long; *M. gregorii* Camp (Fig. 449). Upper Triassic;

[1] *Abel, O.*, Die Schnautzenverletzungen der Parasuchier und ihre biologische Bedeutung. Palaeont. Zeitschr., vol. v., p. 26, 1922.—*Camp, C. L.*, A Study of the Phytosaurs. Mem. Univ. California, vol. x., 1930.—*Case, E. C.*, Skull of a new form of Phytosaur, with Notes on the Characters of North American Phytosaurs. Univ. Michigan Studies, mem. ii., 1929.—Lower Jaw of *Brachysuchus*. Contrib. Mus. Palaeont. Univ. Michigan, vol. iii., no. 8, 1930.—*Fraas, E.*, Die schwäbischen Trias-Saurier. Stuttgart, 1896.—*Huene, F. von*, Beiträge zur Kenntnis und Beurteilung der Parasuchier. Geol. u. Palaeont. Abhandl., n.s., vol. x., p. 67, 1911.—New Phytosaur from the Palisades near New York. Bull. Amer. Mus. Nat. Hist., vol. xxxii., p. 275, 1913.—Neue Beiträge zur Kenntnis der Parasuchier. Jahrb. preuss. geol. Landesanst., vol. xlii., p. 59, 1922.—*Huxley, T. H.*, *Stagonolepis Robertsoni* (Agassiz). Quart. Journ. Geol. Soc., vol. xv., p. 440, 1859; also *loc. cit.*, vol. xxxi., p. 423, 1875, and Mem. Geol. Surv., monogr. viii., 1877.—*Jaekel, O.*, Über einen neuen Belodonten aus dem Buntsandstein von Bernburg. Sitzb. Ges. naturf. Freunde, Berlin, 1910, p. 197.—*Lees, J. H.*, Skull of *Paleorhinus*. Journ. Geol., vol. xv., p. 121, 1907.—*M'Gregor, J. H.*, The Phytosauria. Mem. Amer. Mus. Nat. Hist., vol. ix., p. 29, 1906.—*Mehl, M. G.*, *Angistorhinus*. Journ. Geol., vol. xxi., p. 186, 1913.—The Phytosauria of the Trias. *Loc. cit.*, vol. xxiii., p. 129, 1915.—New or little known Phytosaurs from Arizona, etc. Quart. Bull. Univ. Oklahoma. n.s., no. 103, 1916.—*Pseudopalatus*. Univ. Missouri Studies, vol. iii., no. 1, 1928.—*Meyer, H. von*, Reptilien aus dem Stubensandstein des Oberen Keupers. Palaeontographica, vol. vii., p. 253, 1861; vol. x., p. 227, 1863; vol. xiv., p. 99, 1865.—*Sinclair, W. J.*, Large Parasuchian from the Trias of Pennsylvania. Amer. Journ. Sci. [4], vol. xlv., p. 457, 1918.

Arizona. Other species in New Mexico and Texas, perhaps also Utah (*Heterodontosuchus* Lucas).

Mystriosuchus Fraas. Cranium high, sharply separated from the slender, subcylindrical snout, which has a spoon-shaped expansion at the end; external narial openings with raised rim, above antorbital vacuities. All teeth round in section, delicately fluted. Four series of dorsal plates of

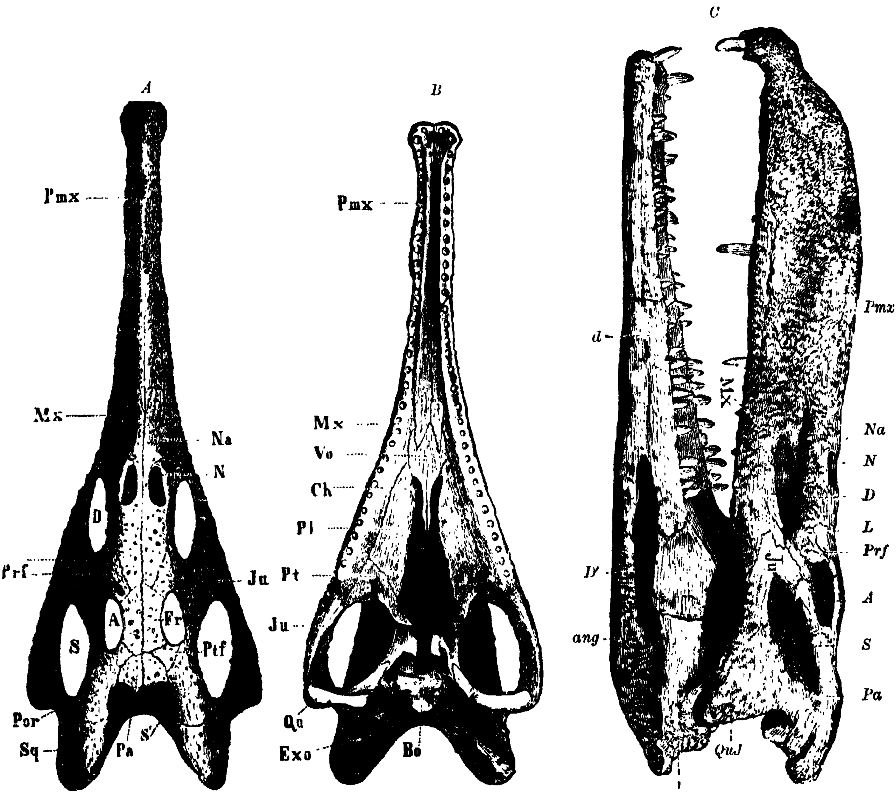


FIG. 448.

Belodon kapffi H. v. Meyer. Middle Keuper; Stuttgart, Würtemberg. Skull from superior (*A*), palatal (*B*), and lateral (*C*) aspects. *A*, orbit; *ang*, angular; *art*, articular; *Bo*, basioccipital; *Ch*, internal nares; *d*, dentary; *D*, antorbital vacuity; *D'*, mandibular vacuity; *Exo*, exoccipital; *Fr*, frontal; *Ju*, jugal; *L*, lachrymal; *Mx*, maxilla; *N*, external narial openings; *Na*, nasal; *Pa*, parietal; *Pl*, palatine; *Pmx*, premaxilla; *Por*, postorbital; *Prf*, prefrontal; *Pt*, pterygoid; *Ptf*, postfrontal; *Qu*, quadrate; *QuJ*, quadrato-jugal; *S*, lateral temporal vacuity; *S'*, supratemporal vacuity; *Sq*, squamosal; *Vo*, vomer. $^1/_7$ nat. size.

nearly equal size; a ventral shield of smaller plates on the throat. Skeleton less stout than in *Belodon*. *M. planirostris* H. von Meyer sp., with skull about 80 cm. long, snout 60 cm. long. Upper Triassic (Keuper); Würtemberg.

Palaeorhinus Williston. Resembling *Mystriosuchus*, but snout relatively shorter and external narial openings further forwards than antorbital vacuities. *P. bransoni* Will., with skull nearly 80 cm. long. Upper Triassic; Wyoming.

Rutiodon Emmons (*Rhytidodon* Cope) (Fig. 451). As *Mystriosuchus*, but

some teeth compressed to sharp edges. Triassic; North Carolina, Pennsylvania, and New Jersey.

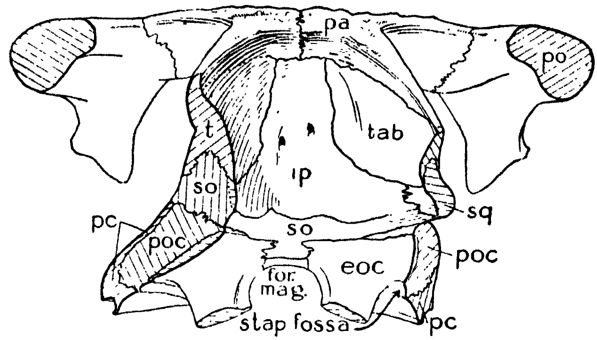


Fig. 449.

Machaeroprosopus gregorii Camp. Imperfect occiput. Upper Triassic; Apache Co., Arizona. *eoc*, exoccipital; *for. mag.*, foramen magnum; *ip*, postparietal; *pa*, parietal; *pc*, prootic process; *po*, postorbital; *poc*, opisthotic (paroccipital); *so*, supraoccipital; *sq*, squamosal; *stap. fossa*, arrow pointing to stapedial fossa; *tab*, tabular. 1/3 nat. size (after Camp).

Fig. 450.

Belodon kapffi H. v. Meyer. Dorsal scute. Middle Keuper; Würtemberg. 1/3 nat. size (after H. v. Meyer).

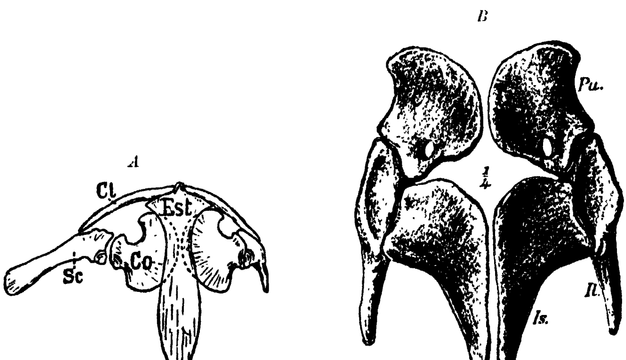


Fig. 451.

Rutiodon carolinensis Emmons. *A*, Pectoral arch. *B*, Pelvis. Both ventral aspect. Triassic; North Carolina. *Cl*, clavicle; *Co*, coracoid; *Est*, interclavicle; *Il*, ilium; *Is*, ischium; *Pu*, pubis; *Sc*, scapula (left in normal position, right turned outwards). Much reduced (after M'Gregor).

Angistorhinus Mehl. As *Palaeorhinus*, but external narial openings above antorbital vacuities; hinder teeth much compressed to sharp edges. *A. grandis* Mehl, with skull 1 m. long. Triassic; Wyoming.

Promystriosuchus, Leptosuchus, Brachysuchus Case. Upper Triassic; W. Texas.

Angistorhinopsis F. von Huene. Rhaetic; Basle, Switzerland, and Salzgitter, N. Germany. Upper Keuper; Halberstadt, N. Germany.

? *Rileya* F. von Huene. Upper Triassic; Bristol.

? *Stagonolepis* Agassiz. Imperfectly known, with pitted dermal plates. Triassic; Elgin, Scotland.

Family 2. **Desmatosuchidae.**[1]

Upper temporal vacuity secondarily closed; a pineal foramen; snout shorter than in Belodontidae. *Bony dermal plates very extensive.* Triassic.

Desmatosuchus Case (Fig. 452). Back completely covered with dermal plates in a broad median paired series and a smaller lateral paired series, each of the latter plates produced into a prominent point; the first five rings covering the foremost ten vertebrae, each other ring covering one vertebra. Triassic; W. Texas.

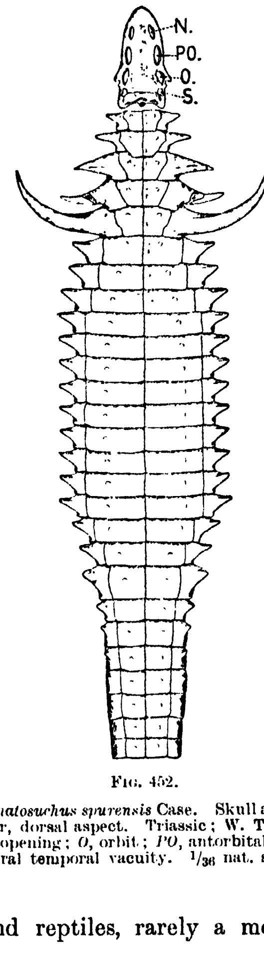


FIG. 452.

Desmatosuchus spurensis Case. Skull and dorsal armour, dorsal aspect. Triassic; W. Texas. *N*, narial opening; *O*, orbit; *PO*, antorbital vacuity; *S*, lateral temporal vacuity. 1/36 nat. size (after Case).

Sub-Order 4. PSEUDOSUCHIA.

Snout small and short, with small premaxillae and large nasals, and a pair of external narial openings laterally placed between these bones; internal nares far forwards; an antorbital vacuity; no pineal foramen; a vacuity in the mandibular ramus. No vertebral intercentra except in atlas and axis. One paired series of bony dermal plates dorsally.

Most of these are small lizard-shaped land reptiles, rarely a metre in length.

Family 1. **Aetosauridae.**[2]

Back completely covered with short and broad bony plates. Triassic.

[1] *Case, E. C.*, Preliminary Description of a new Sub-Order of Phytosaurian Reptiles. Journ. Geol., vol. xxviii., p. 524, 1920.—Endocranial Cast from *Desmatosuchus*. Journ. Compar. Neurology, vol. xxxiii., p. 133, 1921.—*D. spurensis*, in Carnegie Inst. Washington, Publ. no. 321, 1922.

[2] *Emerson, B. K.*, and *Loomis, F. B.*, *Stegomus longipes*. Amer. Journ. Sci. [4], vol. xvii., p. 377, 1904.—*Fraas, E.*, *Aetosaurus crassicauda*. Jahresh. Verein f. vaterl. Naturk. Württ., p. 101, 1907.—*Fraas, O.*, *Aetosaurus ferratus*. *Loc. cit.*, vol. xxxiii., p. 1, 1877.—*Dyoplax arenaceus*. *Loc. cit.*, vol. xxiii., p. 108, 1867.—*Huene, F. von*, *Aetosaurus ferratus*. Acta Zoologica, vol. i., p. 465, 1920; also vol. ii., p. 330, 1921.—*Marsh, O. C.*, New Belodont Reptile (*Stegomus*). Amer. Journ. Sci. [4], vol. ii., p. 59, 1896.

Aëtosaurus O. Fraas (Fig. 453). Dorsal and ventral armour of radially ornamented scutes; ventral scutes smaller than the dorsal, and almost square. Skull triangular, acuminate in front. Antorbital vacuities large, separated from the large external nares by a narrow ascending process of the maxilla. Twenty-five presacral vertebrae. Interclavicle blade-like. *A. ferratus* O. Fraas, about 85 cm. long. Twenty-four complete but slightly crushed individuals are preserved on a single slab of Stuben Sandstone (Middle Keuper), from

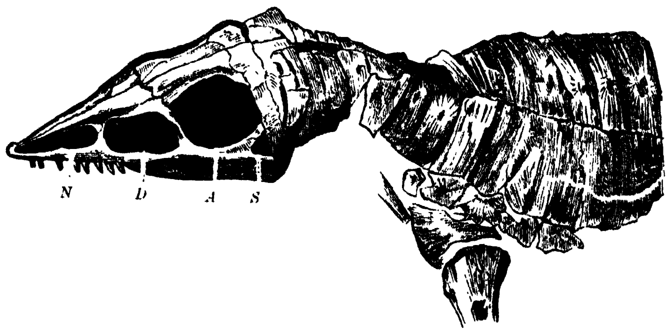


FIG. 453.
Aëtosaurus ferratus Fraas. Head and anterior portion of trunk. Middle Keuper; Heslach, near Stuttgart. *A*, orbit; *D*, antorbital vacuity; *N*, narial opening; *S*, lateral temporal vacuity. ½ nat. size (after O. Fraas).

Heslach, near Stuttgart, now in the Stuttgart Museum. *A. crassicauda* E. Fraas, about 1·5 m. long. Middle Keuper; Pfaffenhofen.

Dyoplax O. Fraas. Middle Keuper; Stuttgart. *Typothorax* Cope. Triassic; New Mexico.

Stegomus Marsh; *Stegomosuchus* F. von Huene (for *Stegomus longipes* Emerson and Loomis). Triassic; Connecticut and Massachusetts.

Shepardia, *Batrachopus*, *Cheirotheroides* Hitchcock. Footprints. Triassic; Connecticut.

Family 2. **Ornithosuchidae.**[1]

Dorsal bony plates relatively small and narrow. Triassic.

Ornithosuchus Newton. Skull pointed in front, very similar to that of *Aëtosaurus.* Teeth slightly recurved, with finely serrated anterior and posterior cutting edges; three in premaxilla, nine in maxilla, and two mandibular teeth overlapping the gap between these two series. Vertebral centra elongated, with very stout neural spines; one presacral vertebra added to sacrum. Ilium elongated, ischium slender, pubis long and rod-like. Limbs longer than in *Aëtosaurus.* *O. woodwardi* Newton; *O. taylori* Broom. Triassic; Elgin, Scotland.

Erpetosuchus Newton. Skull narrow and rounded in front. Dorsal scutes coarsely sculptured. Triassic; Elgin, Scotland.

Euparkeria Broom (Fig. 454). Skull narrow and rounded in front. Three teeth in premaxilla, twelve in maxilla, and one mandibular tooth overlapping

[1] *Boulenger, G. A.*, *Ornithosuchus.* Phil. Trans. Roy. Soc., vol. cxcvi. B, p. 182, 1903.—*Broom, R.*, South African *Euparkeria* and Allied Genera. Proc. Zool. Soc., 1913, p. 619.—*Huene, F. von*, Neue Pseudosuchier, etc. Acta Zoologica, vol. ii., p. 329, 1921.—*Newton, E. T.*, Reptiles from the Elgin Sandstone. Phil. Trans. Roy. Soc., vol. clxxxv. B, p. 573, 1894.

the gap between these two series. A postparietal bone identified by Broom. *E. capensis* Broom, with skull about 9 cm. long. Upper Triassic (*Cynognathus* Zone); Aliwal North, S. Africa.

Browniella Broom. Upper Triassic; Aliwal North.

Saltoposuchus F. von Huene. Middle Keuper; Würtemberg.

Synaptichnium Nopcsa. Footprints from English Upper Triassic.

Cheirotherium Kaup (Fig. 455).[1] Footprints shaped much like prints of the human hand, but with the fifth digit simulating the opposable thumb; those of the fore foot much smaller than those of the hind foot. The skin covered with fine epidermal scales or tubercles; the claws powerful. In all known cases the prints were made on soft mud, and they are preserved only in relief on the overlying slab of sandstone or hard shale. They are often accompanied by sun-cracks. *C. barthi* Kaup, with hind foot nearly 25 cm. long, and other species in the Lower Triassic (Bunter Sandstone) of Thuringia, Franconia, France (Hérault), and Spain (Aragon), and in the Upper Triassic (Keuper) of Thuringia and England (Cheshire). W. Soergel remarks that in the earlier species the fore limbs are relatively larger than in the later species, which walked almost entirely on the hind limbs.

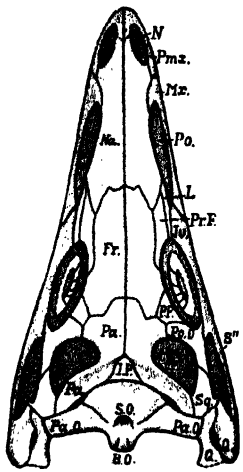


FIG. 454.

Euparkeria capensis **Broom. Skull, dorsal aspect. Upper Triassic; Aliwal North, South Africa. *BO*, basioccipital; *Fr*, frontal; *IP*, postparietal; *Ju*, jugal; *L*, lachrymal; *Mx*, maxilla; *N*, narial opening; *Na*, nasal; *Pa*, parietal; *PaO*, opisthotic + exoccipital; *PF*, postfrontal; *Pmx*. premaxilla; *Po*, antorbital vacuity; *PoO*, postorbital; *PrF*, prefrontal; *Q*, quadrate; *QJ*, quadrato-jugal; *S'*, *S''*, upper and lateral temporal vacuities; *SO*, supraoccipital; *Sq*, squamosal. 2/3 nat. size (after Broom).**

FIG. 455.

Footprints of *Cheirotherium barthi* Kaup. Lower Triassic (Buntsandstein); Hessberg, near Hildburghausen. 1/6 nat. size (after Owen).

Family 3. **Sphenosuchidae.**[2]

Pseudosuchia *without clavicles and with coracoid foramen replaced by a notch.* Rhaetic.

Sphenosuchus Haughton. Premaxillae much reduced, and the paired external narial openings terminal as well as lateral. Ovoid coracoid much

[1] *Soergel, W.*, Die Fährten der Chirotheria; eine palaobiologische Studie. Jena, 1925.

[2] *Broom, R.*, *Sphenosuchus* and the Origin of the Crocodiles. Proc. Zool. Soc., 1927, p. 359.—*Haughton, S. H.*, New Thecodont from the Stormberg Beds. Ann. S. African Mus., vol. xii., p. 98, 1915; also p. 344, 1924.—*Huene, F. von*, Die Bedeutung der *Sphenosuchus*-Gruppe für den Ursprung der Krokodile. Zeitschr. f. indukt. Abstamm.- u. Vererbungslehre, vol. xxxviii., p. 307, 1925.

extended antero-posteriorly. Limbs very slender. *S. acutus* Haughton, with skull nearly 20 cm. long. Rhaetic (Stormberg Beds); Mount Fletcher, Cape Colony, S. Africa.

An imperfect skull (*Proterosuchus fergusi* Broom) from the Karroo Formation (*Procolophon* Zone) of Tarkastad, South Africa, may represent a fourth family of *Pseudosuchia*, with minute teeth on the vomers and pterygoid bones.[1]

Order 12. CROCODILIA.[2]

Amphibious or aquatic reptiles with short neck, a long tail adapted for swimming, and limbs too feeble for habitual support of the body. Roofing bones of the temporal region of the skull contracting into an upper and a lower arch, and the large quadrate firmly fixed; no pineal foramen; a secondary palate formed by the growth of plates from the premaxillary, maxillary, and palatine, often also from the pterygoid bones, which remove the internal narial opening backwards. Teeth with hollow bases and vertical successors, in sockets on the margin of the jaws; no palatal teeth. Vertebrae amphicoelous, amphiplatyan, or procoelous; neural arch united by suture with the centrum; two vertebrae in sacrum. Ribs double-headed, the cervicals and foremost dorsals articulating with both arch and centrum, the others with the arch. Sternum cartilaginous; an interclavicle but no clavicles; coracoid elongated, pierced proximally by a foramen. Abdominal ribs present. Pubis excluded from the acetabulum (which is perforate) by a process of the ischium. Fore limbs nearly always shorter than the hinder pair; hind feet webbed. Usually an armour of pitted bony scutes beneath the horny scales.

In the structure of their heart and brain and in some other features the *Crocodilia* are the highest of existing reptiles, and in their breathing apparatus they exhibit some resemblance to birds. The earliest known genera with a typically Crocodilian pectoral arch (*Notochampsa* Broom; *Pedeticosaurus* Van Hoepen) and a typically Crocodilian pelvic arch (*Erythrochampsa* Haughton), but with comparatively slender limbs, are from the Stormberg Beds (Rhaetic or Lower Jurassic) of South Africa.[3] In the first two genera the skull is imperfectly known, but has an elongated snout with paired terminal nostril. The earliest typical Crocodilians, of Lower Jurassic age, are all aquatic, and throughout the Jurassic and Lower Cretaceous periods they have amphicoelous or amphiplatyan vertebrae and the secondary bony palate extending no further back than the palatine bones (Sub-Order *Mesosuchia* of Huxley). Nearly all the Upper Cretaceous and Tertiary forms resemble the existing *Crocodilia* in having procoelous presacral vertebrae and the secondary bony palate extending back nearly to the hinder edge of the pterygoid bones (Sub-Order *Eusuchia* of Huxley).

[1] *Broom, R.*, New Reptile (*Proterosuchus fergusi*). Ann. S. African Mus., vol. iv., p. 159, 1903.

[2] *Huene, F. von*, Die Bewegungsart der Extremitäten bei Krokodilen. Biol. Centralbl., vol. xxxiii., p. 468, 1913.—*Huxley, T. H.*, Evolution of the *Crocodilia*. Quart. Journ. Geol. Soc., vol. xxxi., p. 423, 1875.—*Mook, C. C.*, Revision of the Mesozoic *Crocodilia* of North America. Bull. Amer. Mus. Nat. Hist., vol. li., p. 319, 1925.—*Nopcsa, F.*, Classification of the *Crocodilia*. Geologica Hungarica, Series Palaeontologica, vol. i., p. 75, 1928.—*Parker, W. K.*, Structure and Development of Skull in *Crocodilia*. Trans. Zool. Soc., vol. xi., p. 263, 1883.

[3] *Broom, R.*, New Crocodilian Genus (*Notochampsa*) from the Upper Stormberg Beds of South Africa. Geol. Mag. [5], vol. i., p. 582, 1904.—*Haughton, S. H.*, Fauna and Stratigraphy of the Stormberg Series. Ann. S. African Mus., vol. xii., p. 358, 1924.

A dorsal armour of bony scutes, overlaid by the horny epidermis, is nearly always present, and there is frequently also a ventral armour. The dorsal scutes are externally pitted, more rarely radially sculptured, and are often longitudinally keeled. The ventral scutes are flattened, keelless, less prominently sculptured, and sometimes divided (Fig. 456).

The vertebral column in the existing *Crocodilia* comprises about twenty-five presacral vertebrae, two sacrals, and at least thirty-five caudals. The presacral vertebrae except the atlas and axis are procoelous, and the sacrals and most anterior caudals are amphiplatyan. The first caudal is convex at both ends. In the *Mesosuchia* all the vertebrae are amphicoelous or amphiplatyan. There are about nine cervicals. The atlas (Fig. 457)

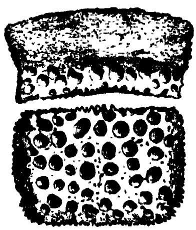


FIG. 456.

Divided ventral scute of *Diplocynodon* sp. Oligocene ; Europe.

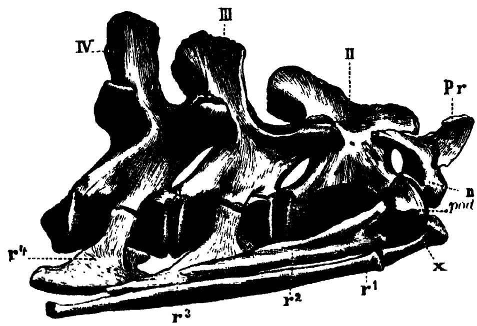


FIG. 457.

Crocodilus vulgaris Cuv. Recent ; Egypt. Anterior cervical vertebrae, I-IV. *n*, lateral piece of atlas ; *pod*, odontoid process (=centrum of atlas) ; *Pr*, proatlas ; r^1-r^4, cervical ribs ; *x*, basal piece of atlas (=intercentrum).

consists of four pieces, and its unpaired ventral piece (x) has been variously interpreted as the centrum, intercentrum, or hypapophysis. The paired lateral elements are roofed by a median dorsal piece which abuts against the occiput and may represent a rudimentary proatlas. The basal piece supports a pair of styliform, single-headed ribs, directed downward and backward. Properly speaking, the atlantal centrum is represented by the odontoid process of the axis. The five to seven succeeding cervicals bear strong neural spines, transverse processes, zygapophyses, parapophyses, and frequently also ventral keels or true hypapophyses. The ribs borne by these vertebrae are all short, hatchet-shaped, and double-headed. In the first two dorsal vertebrae the parapophyses and transverse processes are separated by a narrow interspace, and the latter become more elongated as they are followed backwards. The parapophyses gradually ascend, passing on to the neural arch in the third dorsal vertebra, and thereafter both articular facets for the double-headed ribs are borne by the transverse processes. These facets continue to approximate, and finally become merged with each other in the posterior dorsal vertebrae, so that the last rib is single-headed. The lumbars, of which there are from four to six, have well-developed transverse processes, but bear no ribs. The short and stout sacral ribs are as a rule distally expanded, and suturally united to their centra and neural arches. The vertebrae of the anterior half of the tail bear moderately developed transverse processes, attached like the sacral ribs to the neuro-central sutures.

All except the anterior and a few of the posterior caudals bear chevron bones.

The first and second pairs of dorsal ribs are attached to the sternum, which is a large, rhomboidal, cartilaginous plate lying immediately above and behind the interclavicle (episternum). The succeeding five to seven pairs are connected by means of sternal ribs with the so-called abdominal sternum. The sternal ribs are followed by seven pairs of abdominal ribs, of which the

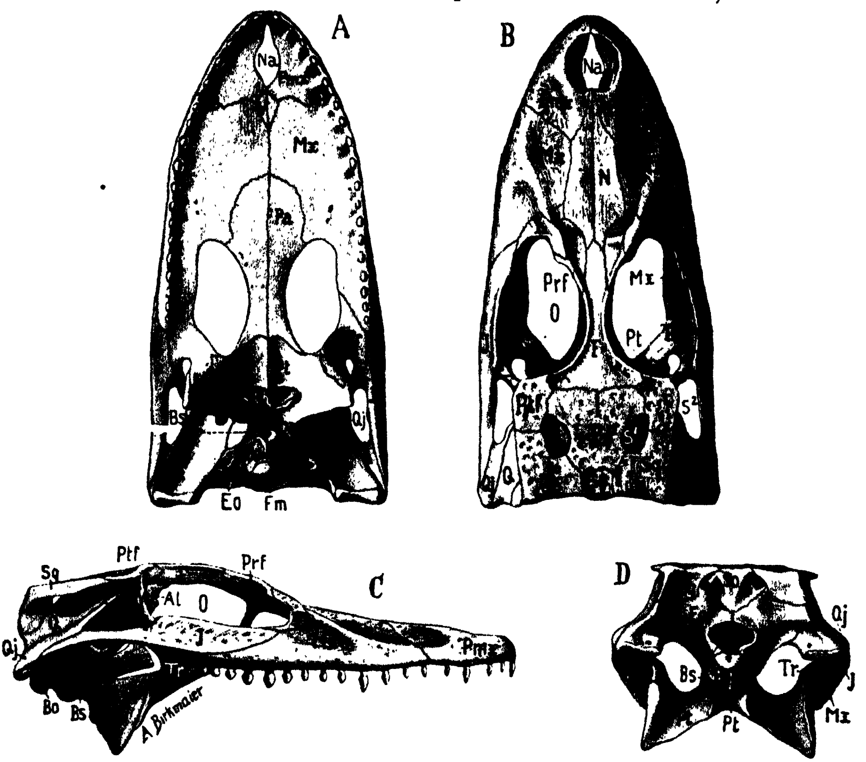


FIG. 458.

Caiman niger Spix. Skull in palatal (*A*), dorsal (*B*), right lateral (*C*), and occipital (*D*) aspects. Recent; Brazil. *Al*, alisphenoid (orbitosphenoid); *Bo*, basioccipital; *Bs*, basisphenoid; *Ch*, internal narial opening; *Eo*, exoccipital; *F*, frontal; *Fm*, foramen magnum; *J*, jugal; *L*, lachrymal; *Mx*, maxilla; *N*, nasal; *Na*, external narial opening and vacuity; *O*, orbit; *P*, parietal; *Pa*, palatine; *Pmx*, premaxilla; *Prf*, prefrontal; *Pt*, pterygoid; *Ptf*, postfrontal; *Q*, quadrate; *Qj*, quadrato-jugal; S^1, S^2, upper and lateral temporal vacuity; *So*, supraoccipital; *Sq*, squamosal; *Tr*, transverse (ectopterygoid); *V*, vomer. $^3/_5$ nat. size.

posterior is the most strongly developed, and unites with the pubic cartilage. Cartilaginous uncinate processes are borne by the dorsal ribs.

The external head bones are almost always coarsely sculptured. The oval or rounded orbits, which in the earliest *Crocodilia* are well enclosed by bone, are in the later forms partly confluent with the lateral temporal vacuities through the inward displacement of the slender postorbital bar. The parietal and frontal are unpaired in the adult, and in the earlier forms the frontal enters the margin of the superior temporal vacuity. There is never a pineal foramen. A small median postparietal has been observed in some young individuals of existing *Crocodilia* and in the Cretaceous *Dyrosaurus*. The

squamosal is a triangular bone forming the postero-external border of the superior temporal vacuity. Postfrontals, prefrontals, and lachrymals are all variable in size. The nasals are long, triangular bones, usually reaching the premaxillae, and sometimes even the external nostril. The narial opening is usually undivided, always terminal, and enclosed by the short, paired premaxillae, sometimes in part by the nasals. The quadrate is broad and immovably united with the surrounding elements.

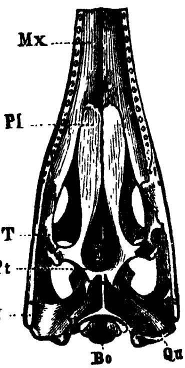


Fig. 459.

Pelagosaurus temporalis Blv. sp. Upper Lias; Curcy, Calvados. Oral aspect of posterior half of skull, showing typical mesosuchian palate. *Bo*, basioccipital; *Ch*, internal nares; *J*, jugal; *Mx*, maxilla; *Pl*, palatine: *Pt*, pterygoid; *Qu*, quadrate. $\frac{1}{2}$ nat. size.

The lower side of the skull (Figs. 458, *A*; 459, 460) is characterised by a great development of the secondary palate, formed by horizontal expansions of the premaxillae, maxillae, and palatines, and in the later *Crocodilia* also of the pterygoids. The palate is pierced by a pair of moderate or large-sized infraorbital vacuities. This extensive roofing of the mouth cavity, which usually conceals the vomers, causes the internal opening of the nasal passage to be displaced far backwards. A transverse bone (ectopterygoid) is present, connecting the pterygoid with the maxilla and jugal (Fig. 460, *T*). Modern gavials exhibit in the adult male a pair of bulbous outgrowths (*bu*) of the palatines which communicate with the nasal passage and function as air-reservoirs (Fig. 460).

The mandibular ramus is composed of the usual six pieces, one of which, the articular, is pneumatic. A large foramen communicating with the inner cavity of the jaw is almost always present between the angular, surangular, and dentary. The symphysis is formed by the latter element alone in the broad-nosed forms, by the dentary and splenial together among the long-nosed species.

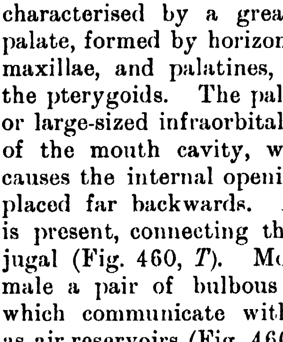


Fig. 460.

Gavialis gangeticus Geoffr. Recent; India. Oral aspect of posterior half of skull, showing eusuchian secondary palate. *Bo*, basioccipital; *bu*, ossified air-chambers; *Ch*, internal nares; *J*, jugal; *Mx*, maxilla; *Pl*, palatine; *Pt*, pterygoid; *Qu*, quadrate; *T*, transverse (ectopterygoid); *X*, opening of eustachian canals.

Numerous conical teeth of oval or circular cross-section, smooth or striated, and frequently carinated, are implanted in deep alveoli along the margin of the jaws. They are often irregular in form and size, but their number remains constant for particular species, and in many cases also for the genus.

In the pectoral arch clavicles are wanting. The scapula is elongated and expanded at either end, as is also the coracoid. The latter is thickened in its proximal portion, and pierced by a round foramen. The humerus is stout, slightly curved, and exhibits near the head a conspicuous process as well as a deltoid crest. Its distal end is furnished with two facets for the bones of the second segment, of which the ulna is generally somewhat the longer (Fig. 461). The proximal row of the carpus contains two elongated elements (radiale and ulnare, both constricted in the middle), and a small pisiforme to which the fifth metacarpal is attached by ligaments. The two radial digits are slightly stouter than the three ulnar digits.

Of the three elements of the pelvic arch (Fig. 462), the pubis is excluded

from the acetabulum, and borne on a prominent anterior process of the ischium. The pubis is long and slender, with a thin distal expansion which scarcely touches its fellow, but adjoins a median unossified plate extending to the posterior abdominal ribs. The ischium meets its fellow in a long median symphysis. The ilium is a strong bone with curved upper margin, and extended antero-posteriorly; its enlarged anterior portion is attached to the sacral ribs. The ischium is sometimes regarded as an ischio-pubis, and the pubis is then identified as a prepubis. The pubis, however, gives attachment to muscles homologous with those of the pubis in *Sphenodon* and *Lacertilia*. The femur is longer and more slender than the humerus, and without an inner trochanter; tibia and fibula are of about equal proportions. There are two rather large proximal tarsals, a calcaneum (fibulare) and astragalo-scaphoid, the latter representing the coössified tibiale, centrale, and intermedium. Two bones are likewise present in the distal row, of which the cuboid is the larger, and supports the third, fourth, and the rudimentary fifth metatarsal. There are only four complete digits, the fifth being represented by its metatarsal. The three inner digits of both pes and manus are provided with claws.

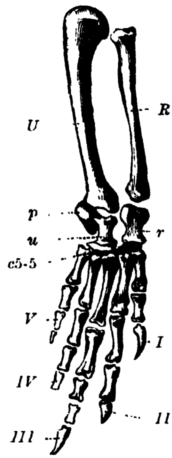


FIG. 461.

Right fore limb of Crocodile. *R*, radius; *U*, Ulna; *c5-5*, distal carpals; *p*, pisiforme; *r*, radiale; *u*, ulnare; *I—V*, digits.

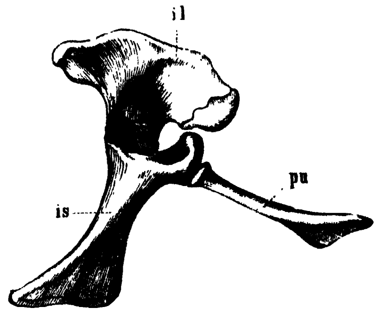


FIG. 462.

Pelvis of Crocodile. *il*, ilium; *is*, ischium; *pu*, pubis.

Sub-Order 1. MESOSUCHIA.

Secondary palate formed by the maxillae and palatines; lateral eustachian tubes forming open grooves on the basisphenoid. Vertebrae amphicoelous or amphiplatyan.

Family 1. **Teleosauridae.**[1]

Snout much elongated. Nasals not reaching the premaxillae and external nostril. Orbits entirely enclosed, superiorly or more rarely laterally directed, and notably smaller than the subrectangular supratemporal vacuities. Postorbital bar not inwardly displaced. Frontal entering margin of supratemporal vacuities. Pre-

[1] *Andrews, C. W.*, Catal. Marine Rept. Oxford Clay, Brit. Mus., pt. ii., p. 80, 1913.—*Auer, E.*, Einige Krokodile der Juraformation. Palaeontographica, vol. lv., p. 217, 1909.—*d'Alton, M.*, and *Burmeister, H.*, Der fossile Gaviale von Boll. Halle, 1854.—*Berckhemer, F.*, Krokodilier des schwäbischen oberen Lias. Neues Jahrb. f. Min., etc., Beil.-Bd. lxiv., p. 1, 1929.—*Bronn, H. G.*, and *Kaup, J. J.*, Ueber die gavialartigen Reptilien der Liasformation. Stuttgart, 1841.—*Collot, L.*, *Teleidosaurus gaudryi*. Mém. Acad. Sci. Dijon [4], vol. x., p. 41, 1906.—*Deslongchamps, E. E.*, Notes paléontologiques. Caen and Paris, 1863–69.—Le Jura Normand. Caen and Paris 1877–78.—*Deslongchamps, J. A. E.*, Mémoire sur les Teléosauriens de l'époque jurassique. Mém. Soc. Linn. Norm., vol. xiii., 1863.—*Nopcsa, F.*, Reptilian Bones from Eocene of Sokoto. Geol. Surv. Nigeria, Occasional Paper no. 2, 1925 [microscopic structure of bones of *Dyrosaurus*, etc.].—*Thevenin, A.*, Le *Dyrosaurus* des Phosphates de Tunisie. Ann. Paléont., vol. vi., p. 95, 1911.

frontals small, lachrymals well developed. Antorbital vacuities small, laterally placed. Teeth conical, slender, closely set. Mandibular rami united in a long symphysis formed by the dentary and splenial. Vertebrae amphicoelous. Fore limbs only about half as long as the hinder pair. Dorsal armour consisting of a paired series of broad, overlapping plates ; ventral plates suturally united, forming several more or less irregular series, or a mosaic of small polygonal scutes. Jurassic ; perhaps surviving until Lower Eocene.

The members of this family, which lived chiefly in the sea, closely resemble modern gavials in size and general appearance, except that they have smaller heads and more weakly developed fore limbs. The principal differ-

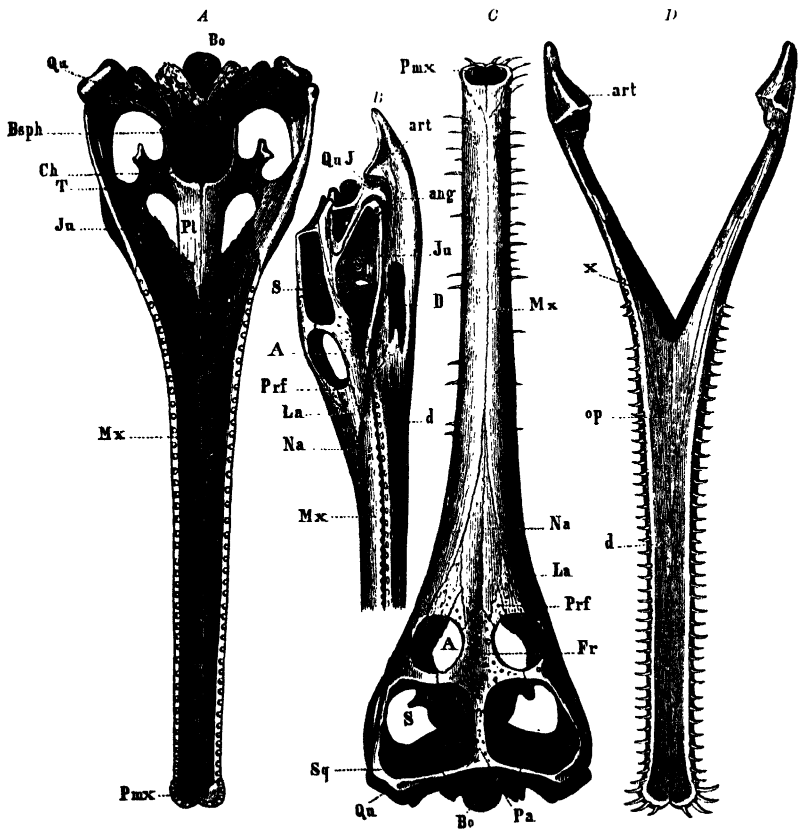


FIG. 463.

Teleosaurus cadomensis Geoffroy. Bathonian ; Caen, Calvados. *A*, Palatal. *B*, Lateral. *C*, Upper aspects of skull. *D*, Mandible. *A*, orbit ; *ang*, angular ; *art*, articular ; *Bo*, basioccipital ; *Bsph*, basisphenoid ; *Ch*, internal nares ; *D*, mandibular vacuity ; *d*, dentary ; *Fr*, frontal ; *La*, lachrymal ; *Mx*, maxilla ; *Na*, nasal ; *op*, splenial ; *Pa*, parietal ; *Pl*, palatine ; *Pmx*, premaxilla ; *Prf*, prefrontal ; *Qu*, quadrate ; *QuJ*, quadrato-jugal ; *S*, supratemporal vacuity ; *S'*, lateral temporal vacuity ; *Sq*, squamosal ; *T*, transverse (ectopterygoid) ; *x*, surangular. About $^1/_3$ nat. size (after E. Deslongchamps).

ences are to be found in the characters of the palate, eustachian passages, vertebral centra, ventral armour, and absence of hypapophyses in the cervical region.

Mystriosaurus Kaup. Snout gradually tapering and premaxillary region expanded; orbits directed upwards; superior temporal fossae elongated.

Ventral border of internal nares angulated, the palatines meeting in the middle line at an acute angle. Teeth implanted nearly vertically, with anterior and posterior carinae. Tracheal rings sometimes preserved (figured by Branca as vertebrae of a swallowed reptile in Abhandl. k. preuss. Akad. Wiss., phys.-math. Cl., 1907, pl. i., fig. 1, 1908). The swimming membrane between the toes of the fore and hind feet also sometimes preserved. Known by complete skeletons from the Upper Lias of Würtemberg, Franconia, and

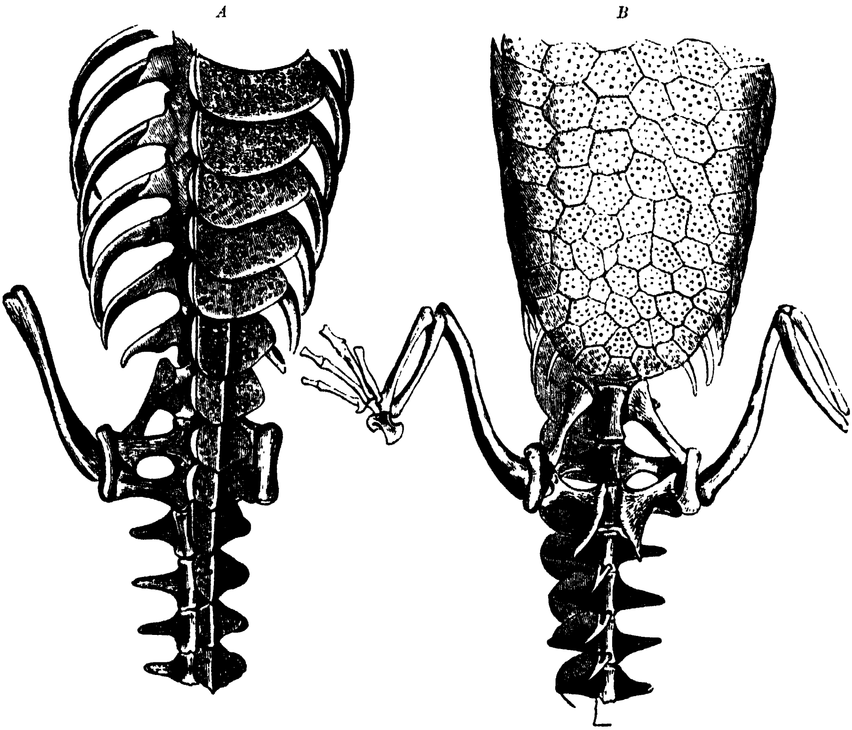


FIG. 464.

Teleosaurus cadomensis Geoffroy. Bathonian; Caen, Calvados. Portion of dorsal (*A*), and ventral (*B*) armour with vertebrae, pelvis, and hind limbs (restored by E. Deslongchamps).

England. *M. bollensis* Jäger sp.; *M. chapmani* König sp. Skull attaining a length of 1 m., and total length upwards of 6 m.

Pelagosaurus Bronn (Fig. 459). Like the preceding, but much smaller, the snout tapering more gradually, and orbits laterally directed. Sclerotic plates present. Antorbital vacuity much reduced or absent; suborbital vacuity in the palate large; internal narial opening of pyriform outline. *P. typus* Bronn, about 1 m. in length; some species 2 m. Upper Lias of Southern Germany, England, and France.

Steneosaurus Geoffroy (*Leptocranius* Bronn; *Sericodon* H. v. Meyer). Differs from *Mystriosaurus* in having the internal narial opening rounded, palatines more expanded, and frontal small. Dorsal scutes united by peg-and-socket joint. Bathonian to Kimmeridgian of Europe; Middle Jurassic of Madagascar. *S. leedsi* Andrews, known by nearly complete skeleton, with

skull 85 cm. long, from Oxford Clay, Peterborough. Nine or ten cervical, fifteen dorsal, two sacral, and about forty caudal vertebrae.

Mycterosuchus Andrews. As *Steneosaurus*, but snout suddenly narrowed in front of orbits, and dermal scutes thicker. *M. nasutus* Andrews, with skull 1 m. long. Oxford Clay; Peterborough.

Teleosaurus Geoffroy (Figs. 463, 464). Skull much elongated and narrow; snout flattened, thin, with rectilinear edges; teeth curved outwards; orbits circular, directed upwards. Dorsal scutes longitudinally keeled in sacral and caudal regions; ventral armour a mosaic extending between the limb girdles. Lower Jurassic. *T. cadomensis* Geoffroy.

Aeolodon H. v. Meyer. Upper Jurassic. *Teleidosaurus* Deslongchamps. Bathonian; N. France.

Dyrosaurus Pomel. Skull essentially Teleosaurian, but nasals extended perhaps to the narial opening. *D. phosphaticus* P. Thomas sp., with skull about 1 m. long, from Lower Eocene (Paleocene), Gafsa, Tunis. Fragments probably of this genus also in Paleocene of the Sudan, Nigeria, and Togoland.

Eggs apparently of Teleosaurians are known from the Upper Lias of Whitby and the Great Oolite of Cirencester (*Oolithes bathonicae* Buckman).[1]

Family 2. **Pholidosauridae.**[2]

As Teleosauridae, *but supratemporal vacuities relatively small, postorbital bar inwardly displaced, nasals extending forwards to premaxillae, internal nares further back, and fore limbs relatively larger.* Upper Jurassic and Cretaceous, perhaps also Lower Eocene.

The members of this family are known chiefly from estuarine and fresh-water deposits in the Purbeckian, Wealden, and Lower Cretaceous in Europe, Upper Cretaceous of North America, and perhaps Eocene of West Africa.

Pholidosaurus H. v. Meyer (*Macrorhynchus* Dunker). Teeth round or oval in section, longitudinally striated, in uniform series of about thirty on each side in either jaw. Ventral armour a mosaic of polygonal scutes. Purbeckian and Wealden of England, and Neocomian (Hils Sandstone) of Hanover.

Petrosuchus Owen. Purbeckian; Dorset.

Crocodileimus Jourdan. Ventral scutes polygonal. Upper Jurassic (Lithographic Stone); Cerin, Ain, France.

Teleorhinus Osborn. *T. browni* Osb., with skull 1 m. long. Upper Cretaceous (Fort Benton Group); Montana.

? *Hyposaurus* Owen. Upper Cretaceous; New Jersey.

? *Wurnosaurus, Rhabdognathus, Sokotosaurus* Swinton. Fragments of rostrum found with specialised Teleosaurian vertebrae. Lower Eocene; Nigeria.

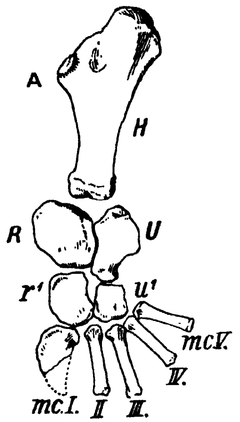
? *Congosaurus* Dollo. Ventral scutes quadrangular, in imbricating transverse rows. *C. bequaerti* Dollo, with skull 70 cm. long. Lower Eocene (Paleocene); Landana, Congo.

[1] *Buckman, J.*, Fossil Reptilian Eggs from the Great Oolite of Cirencester. Quart. Journ. Geol. Soc., vol. xvi., p. 107, 1860.—*Melmore, S.*, Reptilian Egg from the Lias of Whitby. Ann. Rep. Yorks. Phil. Soc., 1930.

[2] *Andrews, C. W.*, Skull and Part of Skeleton of a Crocodile from the Middle Purbeck of Swanage, etc. Ann. Mag. Nat. Hist. [8], vol. xi., p. 485, 1913.—*Dollo, L.*, La Découverte de Téléosauriens Tertiaires au Congo. Bull. Acad. Roy. Belg., Cl. Sci., no. 7, p. 288, 1914.—*Osborn, H. F.*, *Teleorhinus browni.* Bull. Amer. Mus. Nat. Hist., vol. xx., p. 239, 1904.—*Swinton, W. E.*, Fossil Reptilia from Sokoto Province. Geol. Surv. Nigeria, Bull. no. 13, 1930.—*Watson, D. M. S.*, Mem. and Proc. Manchester Lit. and Phil. Soc., vol. lv., mem. 18, 1911.

Family 3. **Metriorhynchidae.**[1] (*Thalattosuchia* E. Fraas.)

Snout elongated. Nasals relatively large, sometimes reaching the premaxillae. Frontal entering margin of supratemporal vacuities. Prefrontals very large and overhanging the orbits, which are directed forwards and outwards. Sclerotic plates present. Orbit separated from the lateral temporal vacuity by a slender, inwardly displaced postorbital bar. Teeth conical and carinate, usually laterally compressed. Vertebrae amphiplatyan or slightly amphicoelous. Fore limb greatly reduced and paddle-like. Hind limb large. Tail long, the end bent downwards and bearing a caudal fin. No dermal armour. Middle and Upper Jurassic, and Lower Cretaceous.



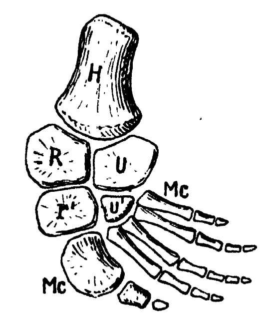


Fig. 465.

Fore limbs of *Metriorhynchidae*. *A*, *Metriorhynchus* sp. Left fore limb. Oxford Clay; Peterborough. About 4/5 nat. size (after Andrews). *B*, *Geosaurus suevicus* E. Fraas. Fore limb modified into a paddle. Lithographic Stone; Würtemberg. 1/3 nat. size (after E. Fraas). *H*, humerus; *mc.I.–V.*, metacarpals; *R*, radius; r^1, radiale; *U*, ulna; u^1, ulnare.

These Mesosuchian crocodiles were completely adapted for life in the open ocean.

Metriorhynchus H. v. Meyer (*Suchodus* Lydekker) (Fig. 465, *A*). Skull gradually tapering without expansion at end of snout, feebly sculptured. External nostril large, upwardly directed. Teeth not serrated, from sixteen to forty on each side of each jaw according to the length of the snout; three pairs in the premaxillae, the hinder two relatively large. Seven cervical, about seventeen dorsal, one or two lumbar, two sacral, and not less than thirty-five caudal vertebrae. *M. superciliosum* Blv. sp., *M. moreli* Deslong., and other species. Oxfordian and Kimmeridgian; England and N. France. Also Patagonia.

Geosaurus Cuvier (*Halilimnosaurus* Ritgen; *Cricosaurus* Wagner; *Rhacheosaurus* H. von Meyer) (Fig. 465, *B*). Teeth finely serrated. Seven cervical, about eighteen dorsal, two lumbar, two sacral, and about fifty caudal vertebrae, of which twenty-seven are in front of the downward bend for the caudal fin. Fore paddle shorter and broader than in *Metriorhynchus*. *G. giganteus* Sömmering sp., and other species from 2 m. to 2·5 m. in length. Upper Jurassic (Lithographic Stone); Bavaria and Würtemberg.

[1] *Ammon, L. von*, Jurassische Krokodile aus Bayern. Geogn. Jahresh., München, Jahrg. 18, p. 62, 1905.—*Andrews, C. W.*, Catal. Marine Rept. Oxford Clay, Brit. Mus., pt. ii., pp. x, 143, 1913; also Geol. Mag. [6], vol. ii., p. 444, 1915.—*Arthaber, G. von*, Organisation und Anpassungserscheinungen des Genus *Metriorhynchus*. Beitr. Paläont. Österr.-Ungarns, vol. xix., p. 287, 1906; also Centralbl. f. Min., etc., 1907, pp. 385, 502.—*Auer, E.*, Genus *Metriorhynchus*. Centralbl. f. Min., etc., 1907, pp. 358, 536.—*Broili, F.*, Beobachtungen an *Geosaurus*. Centralbl. f. Min., etc., 1931, Abt. B, p. 232.—*Fraas, E.*, Die Meer-Crocodilia (*Thalattosuchia*) des oberen Jura. Palaeontographica, vol. xlix., p. 1, 1902.—*Nopcsa, F.*, Systematische Stellung von *Neustosaurus*-Raspail. Centralbl. f. Min., etc., 1903, p. 504.—*Piveteau, J.*, Le Reptile de Gigondas et l'évolution des Métriorhynchidés. Ann. Paléont., vol. xvii., p. 30, 1928.—*Schmidt, W. E.*, *Metriorhynchus jaekeli*, nov. sp. Zeitschr. Deutsch. Geol. Ges., vol. lvi., Protokolle, p. 97, 1904.

Dakosaurus Quenstedt (*Plesiosuchus* Owen). Perhaps identical with *Metriorhynchus*. Skull comparatively short and broad. Teeth not serrated. Middle and Upper Jurassic; Würtemberg and Bavaria. Kimmeridgian; England and France. A nearly complete skeleton of *D. maximus* Plien. sp., 4 m. long, in the Stuttgart Museum.

Neustosaurus Raspail. Neocomian; Vaucluse.

Enaliosuchus Koken. Neocomian; N. Germany.

Family 4. **Atoposauridae.**

Lizard-shaped small Mesosuchians with a broad, triangular skull. Orbits larger than supratemporal vacuities; narial opening sometimes divided by premaxillae and nasals; postorbital bar slender and inwardly displaced. Limbs long and slender. Dorsal armour narrow, consisting of a paired longitudinal series of oblong plates; no ventral armour. Upper Jurassic.

Alligatorium Jourdan. External cranial bones coarsely sculptured; hind limbs longer and more robust than the anterior pair. Total length about

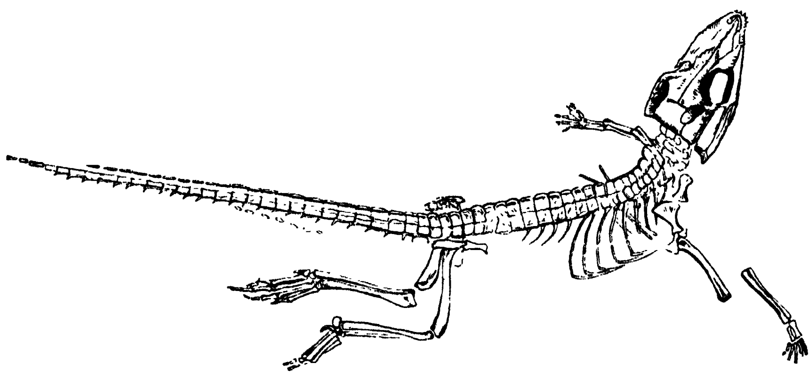


FIG. 466.
Alligatorellus beaumonti Jourdan. Upper Jurassic; Cerin, Ain, France. 1/2 nat. size.

40 cm. Lithographic Stone; Cerin, France; Montsech, Lérida, Spain; and Bavaria.[1]

Alligatorellus Jourdan (Fig. 466). Cranial bones faintly sculptured. Tail very long; at least thirty caudals. *A. beaumonti* Jourd., 22 cm. long. Lithographic Stone; Cerin, France.

Atoposaurus H. v. Meyer. Tail very long, comprising over fifty caudals. Lithographic Stone; Cerin, France; and Bavaria.

Family 5. **Goniopholidae.**[2] (*Metamesosuchia* Hulke.)

Snout short or moderately long and broad. Orbits sometimes smaller than supratemporal vacuities, of which the frontal enters the margin. Postorbital bar

[1] *Broili, F.*, Die Gattung *Alligatorium* im oberen Jura von Franken. Sitzb. Bay. Akad. Wiss., math.-naturw. Abt., 1931, p. 63.

[2] *Dollo, L.*, Première Note sur les Crocodiliens de Bernissart. Bull. Mus. Roy. d'Hist. Nat. Belg., vol. ii., p. 309, 1883.—*Holland, W. J.*, New Crocodile from Jurassic of Wyoming. Ann. Carnegie Mus., vol. iii., p. 431, 1905.—*Hooley, R. W.*, Skull and Skeleton of *Goniopholis crassi-*

slender and inwardly displaced. Internal narial opening at hinder margin of palatines and bounded in part by the pterygoids. Dorsal armour comprising two or more longitudinal series of overlapping and sometimes articulating scutes; ventral armour present. Upper Jurassic and Cretaceous.

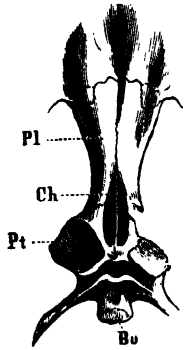


FIG. 467.
Goniopholis simus Owen. Purbeckian; Swanage, Dorset. Posterior portion of palate. *Bo*, basioccipital; *Ch*, internal nares; *Pl*, palatine; *Pt*, pterygoid. 1/8 nat. size (after Hulke).

Goniopholis Owen (*Diplosaurus* Marsh; *Amphicotylus* Cope) (Fig. 467). Snout moderately long, nasals not quite reaching external nostril; supratemporal vacuities larger than the orbits. Teeth stout, carinated and vertically grooved. Dorsal scutes united by peg-and-socket articulation. Ventral armour consisting of seven to ten longitudinal series of polygonal plates united by jagged sutures. *G. crassidens* Owen, with skull 55 cm. long, from English Wealden. *G. simus* Owen, known by complete skeletons about 2 m. long, has limbs of equal size. Purbeckian and Wealden; England, Belgium, and Northern Germany. Other species in Upper Jurassic and Lower Cretaceous of North America and Brazil; and U. Cretaceous, New Mexico.

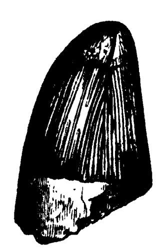


FIG. 468.
Machimosaurus hugii v. Meyer. Kimmeridgian; Lindnerberg, near Hanover. Nat. size.

Coelosuchus Williston. Upper Cretaceous; Wyoming.

Bernissartia Dollo. Supratemporal vacuities smaller than the orbits; nasals not reaching the external nostril. Twenty irregular teeth on each side of either jaw; fore limbs much shorter than the hinder pair. Dorsal armour with more than two longitudinal series of overlapping scutes; ventral scutes also overlapping. *B. fagesi* Dollo, 1 m. long. Wealden; Belgium.

Machimosaurus H. v. Meyer (Fig. 468). Teeth obtusely conical, strongly striated. Upper Jurassic; Europe.

Nannosuchus Owen. Dwarf crocodiles similar to *Goniopholis*, but with slender, curved, smooth, and more uniform teeth. Skull about 10 cm. long. Purbeckian; Dorset. *Oweniasuchus* A. S. Woodw. (*Brachydectes* Owen). Ibid.

Theriosuchus Owen. General form approaching that of modern crocodiles. Supratemporal vacuities smaller than the orbits; teeth tumid and very irregular; mandibular symphysis short. Dorsal scutes overlapping and also united at their outer angles by peg-and-socket articulations; ventral scutes polygonal, united by sutures only. *T. pusillus* Owen, less than 50 cm. long. Purbeckian; Dorset.

? *Symptosuchus* Ameghino; *Microsuchus* Dolgopol de Saez. Cretaceous; Patagonia.

? *Doratodon* Seeley. Upper Cretaceous; Gosau, Austria.

dens. Quart. Journ. Geol. Soc., vol. lxiii., p. 50, 1907.—*Hulke, J. W.*, Two Skulls from the Wealden and Purbeck Formations. Quart. Journ. Geol. Soc., vol. xxxiv., p. 377, 1878.—*Mook, C. C.*, Revision of Mesozoic Crocodilia of North America. Bull. Amer. Mus. Nat. Hist., vol. li., p. 319, 1925.—*Owen, R.*, Reptiles of Wealden and Purbeck Formations, Supplements viii., ix. Palaeont. Soc., 1878-79.—Association of Dwarf Crocodiles with the Diminutive Mammals of the Purbeck Shales. Quart. Journ. Geol. Soc., vol. xxxv., p. 148, 1879.—*Williston, S. W.*, American Amphicoelian Crocodiles. Journ. Geology, vol. xiv., p. 1, 1906.—*Woodward, A. S.*, *Goniopholis hartti* from Bahia (Brazil). Quart. Journ. Geol. Soc., vol. lxiii., p. 132, 1907.

Family 6. **Notosuchidae.**[1]

Snout very short, and quadrate bone only slightly inclined backwards. Orbits much larger than the superior temporal vacuities, and the frontal excluded from the latter by the union of the parietal with the postfrontals. Postorbital bar slender and inwardly displaced. Vacuity in mandibular ramus very large. No dermal armour. Cretaceous (? and Upper Jurassic).

Notosuchus A. S. Woodward. Head bones nearly smooth. Large nasals reaching single narial opening, which is directed forwards. A small antorbital vacuity. Three incisiform and one caniniform tooth in premaxilla, seven nearly uniform teeth in maxilla; no lower canine. Fore limb not much smaller than hind limb. *N. terrestris* A. S. Woodw., with skull 18 cm. long. Probably Upper Cretaceous; Neuquen, Patagonia.

Cynodontosuchus A. S. Woodward. Lower canines working on upper canines. Same locality.

Libycosuchus Stromer (Fig. 469). Nasals dividing the narial opening into two laterally directed nares. No antorbital vacuity. *L. brevirostris* Stromer (Fig. 469), with skull about 18 cm. long. Cenomanian ; Egypt.

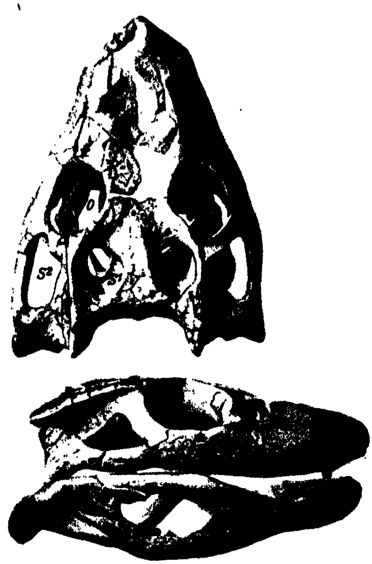


Fig. 469.

Libycosuchus brevirostris Stromer. Skull and mandible, upper and right lateral aspects. Cenomanian ; Egypt. *N*, narial opening ; *O*, orbit ; S^1, S^2, upper and lateral temporal vacuities. $^1/_4$ nat. size (after Stromer).

? *Hoplosuchus* Gilmore. Upper Jurassic (Morrison Formation) ; Utah, U.S.A.

Sub-Order 2. EUSUCHIA.

Secondary palate formed by plates from the maxillae, palatines, and pterygoids ; lateral eustachian tubes piercing the basisphenoid ; postorbital bar slender and inwardly displaced. Presacral vertebrae procoelous.

This group comprises most Cretaceous and Tertiary, and all modern crocodiles, among which some are long-snouted forms, but most are of the broad-snouted type.

[1] *Gilmore, C. W.*, New Aetosaurian Reptile from the Morrison Formation. Ann. Carnegie Mus., vol. xvi., p. 325, 1926.—*Stromer, E. von*, Wirbeltierreste der Baharije-Stufe. Abhandl. k. bay. Akad. Wiss., math.-phys. Kl., vol. xxvii., no. 3, 1914.—*Woodward, A. S.*, Two Mesozoic Crocodilians from the Red Sandstones of Neuquen. Anales Mus. La Plata, Palaeont. Argent., no. 4, 1896 ; also Outlines of Vertebrate Palaeontology, p. 221, 1898.

Family 1. **Hylaeochampsidae.**[1]

Primitive small Eusuchia, *with the large transverse bone of the palate bifurcating, leaving a vacuity between it and the jugal and maxilla.* Wealden.

Hylaeochampsa Owen (*? Heterosuchus* Seeley). Skull of *H. vectensis* Owen about 10 cm. wide at occiput. The procoelous vertebrae named *Heterosuchus valdensis* Seeley, probably belong to the same genus. English Wealden.

Family 2. **Stomatosuchidae.**[2]

Skull broad and flat, with preorbital region very much elongated. Superior temporal vacuities very small, and frontals excluded from them; orbits far back and directed upwards. Mandible toothless, with weak symphysis. Cervical vertebrae without hypapophyses. Upper Cretaceous.

The shape of the mandible seems to show that these crocodiles had a mandibular pouch like that of a pelican.

Stomatosuchus Stromer. Upper jaw with small teeth. Lower border of mandible with wing-like bony process for support of pouch. *S. inermis* Stromer, with skull about 2 m. long. Lower Cenomanian; Baharije, Egypt.

Family 3. **Tomistomidae.**[3] (*Rhynchosuchidae.*)

Snout much produced, passing gradually into the facial region. Nasals long and narrow, their anterior ends intercalated between slender processes of the premaxillae, but not reaching the external nostril. Prefrontals small, lachrymals large. Orbits irregularly oval, about as large as or larger than the superior temporal vacuities. Splenials entering the elongated mandibular symphysis, which bears about fifteen pairs of teeth. Ventral armour absent. Upper Cretaceous to Recent.

The Upper Cretaceous genera, *Thoracosaurus* and *Holops*, retain the primitive character of the frontal entering the margin of the superior temporal vacuities.

Thoracosaurus Leidy (*Sphenosaurus* Ag.). Premaxillae spatulate in form, lachrymals unusually large. Superior temporal vacuity transversely oblong, slightly larger than the orbits; small antorbital vacuity present. About twenty-four curved teeth on either side in each jaw. Upper Cretaceous; New Jersey, Holland, France, and southern Sweden.

[1] *Andrews, C. W.*, Note on the Skull of *Hylaeochampsa*. Ann. Mag. Nat. Hist. [8], vol. xi., p. 492, 1913.

[2] *Nopcsa, F.*, Neue Beobachtungen an *Stomatosuchus*. Centralbl. f. Min., etc., 1926, Abt. B, p. 212.—*Stromer, E. von*, Wirbeltierreste der Baharije-Stufe. Abhandl. Bayer. Akad. Wiss., math.-naturw. Abt., vol. xxx., no. 6, 1925.

[3] *Dollo, L.*, *Kosuchus lerichei*. Bull. Soc. Belge Géol., etc., vol. xxi., Proc.-Verb., p. 83, 1907. —*Joleaud, L.*, Les Crocodiliens du Pliocene d'Eau douce de l'Omo (Éthiopie). Livre Jubil. 1830-1930, Soc. Géol. France, vol. ii., p. 411, 1930.—*Koken, E.*, *Thoracosaurus macrorhynchus* Bl. aus der Tuffkreide von Maastricht. Zeitschr. Deutsch. Geol. Ges., vol. xl., p. 754, 1888.—*Mook, C. C.*, Skull Characters and Affinities of *Gavialosuchus americana* (Sellards). Bull. Amer. Mus. Nat. Hist., vol. xliv., p. 33, 1921; also Amer. Mus. Novit., no. 155, 1924.—*Piveteau, J.*, *Tomistoma macrorhyncha* Blv. sp. Ann. Paléont., vol. xvi., p. 85, 1927.—*Sellards, E. H.*, New Gavial from late Tertiary of Florida. Amer. Journ. Sci. [4], vol. xl., p. 135, 1915; also *loc. cit.*, vol. xlii., p. 237, 1916.—*Toula, F.*, and *Kail, J. A.*, Krokodil-Schädel aus den Tertiärablagerungen von Eggenburg. Denkschr. k. Akad. Wiss. Wien, vol. l., p. 299, 1885.—*Troedsson, G. T.*, Crocodilian Remains from the Danian of Sweden. Lunds Univ. Arsskrift, n.f., vol. xx., avd. 2, 1924; also Geol. Fören. Stockholm Forh., vol. xlv., p. 546, 1924.

Holops Cope. Like the preceding, but without antorbital vacuity, and orbits equal in size with superior temporal vacuities. Upper Cretaceous; New Jersey.

Eosuchus Dollo. Lower Eocene; Erquelinnes, Belgium. Perhaps also fragments in Middle Eocene of Bracklesham, Sussex (*Gavialis dixoni* Owen).

Tomistoma Müller (*Rhynchosuchus* Huxley). Orbits almost twice the size of superior temporal vacuities. Parietals small, lachrymals moderately developed. Internal narial opening rounded. About twenty teeth on either side in each jaw. Eocene; Egypt. Miocene; Hungary, Malta, Sardinia, and Moghara, Egypt. Pliocene; Omo, Ethiopia. Recent in Borneo, Sumatra, and Malay Peninsula.

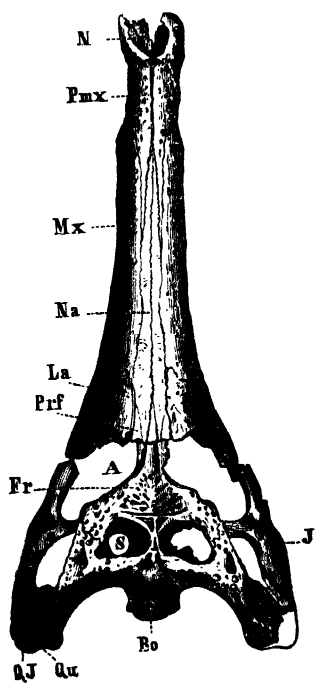


FIG. 470.

Gavialosuchus eggenburgensis Toula and Kail. Miocene; Eggenburg, near Horn, Austria. Dorsal aspect of skull, 1/10 nat. size. Lettering as in Fig. 463.

Gavialosuchus Toula and Kail (Fig. 470). As *Tomistoma*, but anterior edge of internal narial opening angulated. Miocene; Austria, and Florida, U.S.A.

Gryposuchus Gürich. Pleistocene; N. Brazil.

Leptorhamphus, *Oxyodontosaurus* Ambrosetti. Tertiary; Paraná, Argentina.

Family 4. **Alligatoridae.**[1]

Snout broad and short; nasals usually reaching external nostril. Orbits larger than superior temporal vacuities. Mandibular symphysis short. Teeth irregular; the anterior tooth of lower jaw always, and as a rule also the fourth tooth, fitting into pits of the upper jaw. Suture between maxillae and premaxillae on the palate either transverse or convex toward the front. Dorsal armour consisting of more than two rows of scutes, either articulated or lying free in the integument; cervical scutes separated from the dorsal. Ventral armour, when present, comprising numerous series of articulated scutes, each of which consists of two pieces united by suture. Upper Cretaceous to Recent.

In alligators the lower teeth bite entirely within the upper, and the first and fourth lower teeth are received into pits of the upper jaw; but in crocodiles the upper and lower teeth mutually interlock, while the first lower tooth bites into a perforation or pit in the cranium, and the fourth into a lateral notch. Modern alligators inhabit the warmer regions of North and South America and China, and fossil remains occur in the freshwater Cretaceous and Tertiary of both Europe and America.

[1] *Abel, O.*, *Allognathosuchus*, ein an die cheloniphage Nahrungsweise angepasster Krokodiltypus des nórdamerikanischen Eozäns. Palaeont. Zeitschr., vol. ix., p. 367, 1928.—*Gilmore, C. W.*, New Fossil Alligator from the Hell Creek Beds of Montana. Proc. U.S. Nat. Mus., vol. xli., p. 297, 1911.—*Loomis, F. B.*, New River Reptile from the Titanothere Beds. Amer. Journ. Sci. [4], vol. xxxvii., p. 429, 1914.—*Ludwig, R.*, Fossile Krokodilien aus der Tertiärformation des Mainzer Beckens. Palaeontographica, suppl. vol. iii., pts. 4, 5, 1877.—*Mehl, M. G.*, *Caimanoidea visheri*. Journ. Geol., vol. xxiv., p. 47, 1916.—*Mook, C. C.*, *Allognathosuchus*. Bull. Amer. Mus. Nat. Hist., vol. xliv., p. 105, 1921.—*Patterson, B.*, Alligatoroid Genus *Allognathosuchus* in the Lower Oligocene. Field Mus. Nat. Hist. Chicago, publ. 297, Geol. Ser., vol. iv., no. 6, 1931.

Diplocynodon Pomel (Figs. 456, 471). Third and fourth teeth of lower jaw equally enlarged, and either both received into pits of the upper jaw, or the fourth passing into a marginal notch between the maxillae and premaxillae. Dermal armour strongly developed. Abundant in Upper Eocene, Oligocene, and Miocene of England, France, and Germany. Eocene; New Mexico.

Bottosaurus Agassiz. Imperfectly known, but with alligator-like dentition. Upper Cretaceous; New Jersey, Colorado, and Montana.

Brachychampsa Gilmore. Skull from Upper Cretaceous (Hell Creek Beds) of Montana.

Allognathosuchus Mook. With blunt teeth adapted for feeding on Chelonians. Splenial entering mandibular symphysis. *A. polyodon* Cope sp.,

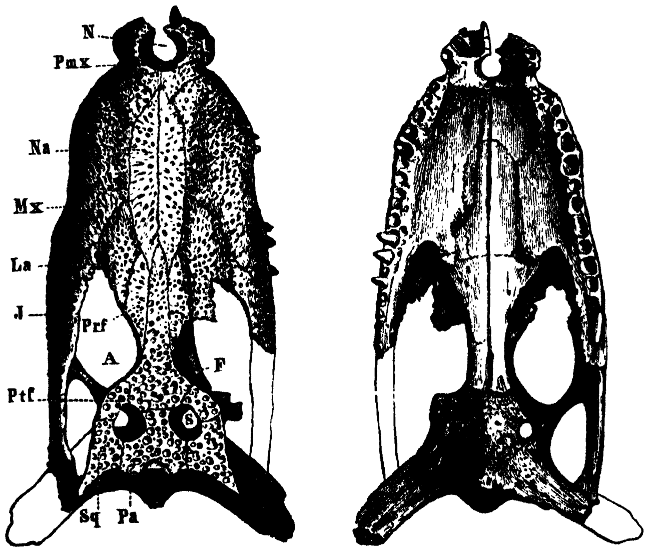


FIG. 471.
Diplocynodon gervaisi Aymard. Superior and palatal aspects of skull, 1/2 nat. size. Oligocene; Ronzon, near Le Puy, France. Lettering as in Fig. 468.

and other species. Eocene and Paleocene; N. America. *A. riggsi* Patterson, from the Lower Oligocene of South Dakota, approaches *Alligator*.

Proalligator Ambrosetti. Tertiary; Paraná, Argentina.

Caimanoidea Mehl. Premaxillary border in front of narial opening very low, so that the nares must have been directed slightly forward. Oligocene; South Dakota.

Alligator Cuvier. Recent; North America and China. Also Lower Pliocene; Nebraska. *Caiman* Spix (Fig. 458); *Jacare* Gray. Recent; Central and South America.

Family 5. **Crocodilidae.**[1]

Snout broad. Orbits larger than superior temporal vacuities. Mandibular symphysis short. Teeth irregular, about nineteen in the upper, and fifteen in the

[1] *Gilmore, C. W.*, *Leidyosuchus sternbergii.* Proc. U.S. Nat. Mus., vol. xxxviii., p. 485, 1910.—*Holland, W. J.*, *Deinosuchus hatcheri.* Ann. Carnegie Mus., vol. vi., p. 281, 1909.—*Lambe, L. M.*, New Crocodilian Genus and Species [*Leidyosuchus canadensis*] from the Judith River Formation of Alberta. Trans. Roy. Soc. Canada [3], vol. i., sect. iv., p. 219, 1908.—*Longman,*

lower jaw on each side, the two series interlocking. Anterior tooth in lower jaw received into a pit, and fourth tooth fitting into a marginal notch of the upper jaw. Suture between maxillae and premaxillae on the palate transverse or concave in front. Dorsal armour comprising more than two rows of scutes lying free in the integument; ventral armour wanting. Upper Cretaceous to Recent.

Crocodilian remains occur abundantly in the freshwater Upper Cretaceous and Tertiaries of Europe and North America, and in the Pliocene of India. Recent species are distributed in tropical Africa, East Indies, New Guinea, Australia, South America, and Cuba.

Leidyosuchus Lambe. Splenial entering the mandibular symphysis. Upper Cretaceous; Alberta, Canada, also Wyoming and South Dakota.

Phobosuchus Nopcsa (*Deinosuchus* Holland *nec* Gervais). Scutes very thick and elevated. *P. hatcheri* Holland, with span of transverse processes of seventh dorsal vertebra measuring 68 cm. Upper Cretaceous (Judith River Beds); Montana.

Allodaposuchus Nopcsa. Danian; Transylvania and S. France.

Crocodilus Laurenti (? *Thecachampsa* Cope) (Figs. 457, 461, 462). Splenial not entering mandibular symphysis. Sixteen to nineteen upper and fourteen to fifteen lower teeth on each side; fifth tooth of maxilla enlarged. Many species in the Tertiary of Europe, North Africa, India, and North America. Pleistocene of Madagascar, Africa, Cuba, Australia, and North America.

Osteoblepharon Schmidt. Frontal just entering margin of superior temporal vacuities. Living in Central Africa.

Dinosuchus Gervais (*Purrusaurus* Barbosa Rodrigues; *Brachygnathosuchus* Mook); *Emysuchus* Nopcsa. Pleistocene; Rio Purus, N. Brazil.

Pallimnarchus De Vis. Pleistocene; Queensland, Australia.

Family 6. Gavialidae.

Snout produced into a long, narrow rostrum, and passing abruptly into the facial region. Nasals separated from premaxillae by a wide interval. Splenials entering the much elongated mandibular symphysis. Teeth twenty-five to thirty on each side of each jaw, approximately uniform, slightly curved and pointed. Tertiary and Recent.

Gavialis Oppel (*Leptorhynchus* Clift; *Rhamphostoma* Wagler) (Fig. 460). Recent in India and Burma. Fossil in Pliocene of Siwalik Hills, India, where it accompanies the gigantic and closely allied *Rhamphosuchus crassidens* Falconer and Cautley (total length 15 m.).

Range and Distribution of the Crocodilia.

Some of the Triassic *Pseudosuchia* closely approach the *Crocodilia*, and one genus (*Sphenosuchus* Haughton) from the Stormberg Beds of South Africa

H. A., A Crocodilian Fossil [*Pallimnarchus pollens*] from Lansdowne Station. Mem. Queensland Mus., vol. viii., p. 103, 1925; also *loc. cit.*, vol. ix., p. 158, 1928.—*Lydekker, R.*, Siwalik Crocodilia. Palaeont. Indica, ser. 10, vol. iii., p. 209, 1886.—*Mook, C. C.*, Skull of the Extinct Madagascar Crocodile, *C. robustus* Vaill. and Grandid. Bull. Amer. Mus. Nat. Hist., vol. xliv., p. 25, 1921.—*Brachygnathosuchus braziliensis*. *Tom. cit.*, p. 43, 1921.—Skull of a Bridger Crocodilian. *Tom. cit.*, p. 111, 1921.—Skull of *Crocodilus acer* Cope. *Tom. cit.*, p. 117, 1921.—Skull Characters of *Crocodilus megarhinus* Andrews. Amer. Mus. Novit., no. 289, 1927.—*Müller, L* Krokodilier des Ægyptischen Tertiärs. Abh. Bay. Akad. Wiss., math.-naturw. Abt., vol. xxxi., no. 2, 1927.—*Nopcsa, F.*, Über die Namen einiger brasilianischer fossiler Krokodile. Centralbl. f. Min., etc., 1924, p. 378.—*Vaillant, L.*, Crocodiliens fossiles tertiaires de St. Gérand-le-Puy. Ann. Sci. Géol., vol. iii., p. 1, 1872.

(probably Rhaetic) seems to have the characteristic Crocodilian pectoral arch. A characteristic Crocodilian pelvic arch (*Erythrochampsa* Haughton) is also known from the Stormberg Beds. The earliest typical crocodiles, however, the *Mesosuchia*, appear in the Upper Lias of England, France, and Germany, and persist essentially unchanged throughout the Jurassic period. In none of them is the secondary palate developed behind the posterior margin of the palatines, there being no outgrowths from the pterygoids; and the vertebrae are amphicoelous, or at most amphiplatyan. Their universal occurrence in marine deposits, the nature of their fossilised stomach-contents and coprolites, and their general organisation, prove them to have been adapted for an exclusively aquatic life. The earliest forms are all longirostral, and it is not until the Upper Jurassic that short- and broad-headed genera with small superior temporal vacuities appear. Owen suggested that the appearance of the latter is correlated with the incoming of warm-blooded prey, and pointed to the association of dwarf crocodiles with small mammals in the Purbeck formation.

Towards the close of the Jurassic changes in external conditions seem to have occurred, for in the Purbeckian and Wealden deposits crocodiles are accompanied for the first time by fresh-water and terrestrial animals suggesting a fluviatile habitat. In the Wealden a few detached crocodilian vertebrae of the procoelous type are found, but it is not until the Upper Cretaceous that typical *Eusuchia* with extended secondary palate and closed eustachian passages become dominant. The *Eusuchia*, like their Upper Jurassic forerunners, comprise both long-snouted and broad-snouted genera, but whether the gavials were derived independently from the modern crocodiles and alligators, or all are traceable to a common Mesosuchian ancestor, is still uncertain. During the Tertiary, alligators and crocodiles lived both in Europe and North America, only becoming extinct in Europe during the Pliocene. The alligators, which appear to have surpassed crocodiles in the Old World, and to have been inferior to them in number in the New, are now restricted to the warmer regions of North and South America and China. Remains of both gavials and crocodiles occur in the Tertiary of India, among which are the most gigantic members of the Order (*Rhamphosuchus*).

Order 13. DINOSAURIA.[1] (*Pachypodes* H. von Meyer; *Ornithoscelida* Huxley.)

Long-tailed and often long-necked reptiles, frequently of considerable and sometimes of gigantic size, with limbs adapted for habitual support of the body. Roofing bones

[1] *Baur, G.*, Der Tarsus der Vögel und Dinosaurier. Morph. Jahrb., vol. viii., p. 417, 1883.—Bemerkungen über das Becken der Vögel und Dinosaurier. *Loc. cit.*, vol. x., p. 613, 1885.—*Branca, W.*, Die Riesengrösse sauropoder Dinosaurier vom Tendaguru, ihr Aussterben und die Bedingungen ihrer Entstehung. Archiv f. Biontologie, vol. iii., p. 73, 1914.—*Cope, E. D.*, Palaeontological Bulletins, nos. 22-28, in Proc. Amer. Phil. Soc., 1876-77.—*Dollo, L.*, Les Dinosauriens adaptés à la vie quadrupède secondaire. Bull. Soc. Belge Géol., vol. xix., Mém., p. 441, 1905.—*Hay, O. P.*, On the Manner of Locomotion of the Dinosaurs, especially *Diplodocus*, with Remarks on the Origin of the Birds. Proc. Washington Acad. Sci., vol. xii., p. 1, 1910.—*Huene, F. von*, Über die Zweistämmigkeit der Dinosaurier, etc. Neues Jahrb. f. Min., etc., Beil.-Bd., xxxvii., p. 577, 1914.—Beiträge zur Geschichte der Archosaurier. Geol. u. Palaeont. Abhandl., n.s., vol. xiii., p. 1, 1914.—Los Saurisquios y Ornitisquios del Cretáceo Argentino. Anales Mus. La Plata, Sección Paleontología, ser. 2, vol. iii., p. 1, 1929.—*Huxley, T. H.*, On the Animals which are most nearly intermediate between Birds and Reptiles. Proc. Roy. Soc., p. 278, 1868. Also Ann. Mag. Nat. Hist. [4], vol. i., p. 220, 1868.—Further evidence on the affinity between the Dinosaurian Reptiles and

of the temporal region of the skull contracting into an upper and a lower arch, and the large quadrate fixed or only slightly movable. No pineal foramen. Teeth in sockets or in a groove on the margin of the jaws; no palatal teeth. Vertebrae opisthocoelous or amphiplatyan, rarely amphicoelous; centrum sometimes hollow or with deep lateral cavities; sacrum comprising from three to ten anchylosed vertebrae. Ribs double-headed. Sternum incompletely ossified; clavicular arch and precoracoid absent. Scapula very large, sometimes coössified with the perforate and anteriorly rounded coracoid. All three pelvic elements entering the acetabulum, which is perforate. Ilium large, antero-posteriorly extended. Ischia usually slender and elongated, frequently united in a median symphysis. Pubis directed downwards and forwards, sometimes developing a postpubic process extending backwards parallel with the ischium. Fore limbs nearly always shorter than the hinder pair; progression very commonly bipedal.

The Order *Dinosauria* comprises Mesozoic reptiles which are extremely varied in organisation, and exhibit several Rhynchocephalian, Crocodilian, and even Avian characters, the latter due chiefly to homoplastic or parallel development. Among the latter, as first noticed by Gegenbaur, the close junction of the astragalus with the tibia, or tendency to form a tibio-tarsus, is an Avian resemblance common to the majority of Dinosaurs.

The earliest known Dinosaurs (*Theropoda*) of Triassic age are shown by their limb structure and footprints to have been mainly bipedal in gait, and by their dentition to have been carnivorous; of the herbivorous Dinosaurs (*Sauropoda* and *Orthopoda*) which range throughout the Jurassic and Cretaceous, some must have been bipedal and others quadrupedal. According to Dollo, the quadrupedal forms have clearly descended from bipedal ancestors. The culmination of the Order occurred during the Upper Jurassic and Cretaceous, in the interval between the decline of Theromorph reptiles and the dominance of the *Mammalia*. During their period of ascendancy many attained proportions far exceeding those of all other known land animals. They had an almost world-wide distribution, and great deposits of their remains occur in Brazil, S.E. Africa, Madagascar, China, and India, as well as in North America[1] and Europe. Though ranging from the Triassic to the Cretaceous in Australia, they appear to be comparatively rare in that region.

Birds. Quart. Journ. Geol. Soc., vol. xxvii., p. 12, 1870.—On the classification of the Dinosauria. *Loc. cit.*, p. 32.—*Lull, R. S.*, Dinosaurian Distribution. Amer. Journ. Sci. [4], vol. xxix., p. 1, 1910.—*Sauropoda* and *Stegosauria* of the Morrison of North America compared with those of Europe and Eastern Africa. Bull. Geol. Soc. America, vol. xxvi., p. 323, 1915.—*Marsh, O. C.*, Numerous contributions in Amer. Journ. Sci. [3], vols. xvi.-l., 1878-96, reprinted in the Dinosaurs of North America. 16th Ann. Rep. U.S. Geol. Surv., 1896.—*Matthew, W. D.*, Dinosaurs. Amer. Mus. Nat. Hist. Handbook, 1915.—*Nopcsa, F.*, Notizen über Dinosaurier: Beiträge zu ihrer Evolution. Centralbl. f. Min., etc., 1918, p. 235.—Primitive Reptilian Fauna in the Uppermost Cretaceous of Hungary. Quart. Journ. Geol. Soc., vol. lxxix., p. 100, 1923.—*Osborn, H. F.*, Reconsideration of the evidence for a common Dinosaur-avian stem in the Permian. Amer. Nat., vol. xxxiv., p. 777, 1900.—*Owen, R.*, A History of British Fossil Reptiles [Reprint from the publications of the Palaeontographical and other Societies], London, 1849-84.—*Romer, A. S.*, The Ilium in Dinosaurs and Birds. Bull. Amer. Mus. Nat. Hist., vol. xlviii., p. 141, 1923.—*Russell, L. S.*, Upper Cretaceous Dinosaur Faunas of North America. Proc. Amer. Phil. Soc., vol. lxix., p. 133, 1930.—*Seeley, H. G.*, *Dinosauria* of the Cambridge Greensand. Quart. Journ. Geol. Soc., vol. xxxv., p. 591, 1879.—Reptile Fauna of the Gosau Formation. *Loc. cit.*, vol. xxxvii., p. 620, 1881. —On the classification of the Dinosauria. Proc. Roy. Soc., vol. xliii., p. 165, 1887.—*Versluys, J.*, Streptostylie bei Dinosauriern, nebst Bemerkungen über die Verwandtschaft der Vögel und Dinosaurier. Zool. Jahrb., Abt. Anat., vol. xxx., p. 175, 1910.

[1] One of the largest North American deposits is that in the Morrison Formation, which is variously regarded as Upper Jurassic or Lower Cretaceous. It is here referred to the Upper Jurassic (see *Simpson, G. G.*, Age of the Morrison Formation. Amer. Journ. Sci. [5], vol. xii., p. 198, 1926).

A bony *exoskeleton* is developed to a varying extent among certain of the *Theropoda* and *Orthopoda*, but in the majority of Dinosaurs the skin was either naked or protected by polygonal and rounded horny scales, not overlapping. The dermal armour, when present, consists either of isolated bony plates or spines, or of interlocking scutes which form a continuous shield encasing portions of the trunk and tail. There are often abdominal ribs in the *Theropoda.*

The *vertebrae* are usually either amphiplatyan or opisthocoelous, more rarely amphicoelous. There are six to seventeen cervicals, ten to eighteen dorsals, usually from three to six, but sometimes as many as ten, fused sacrals, and thirty to seventy caudal vertebrae. The union between the centra and their neural arches is commonly by suture. In the anterior cervicals the neural spines are generally short or rudimentary, and gradually increase in size towards the thoracic region. The atlas and axis, so far as known, much resemble those in crocodiles. All the succeeding cervicals bear double-headed ribs, of which the capitulum is attached to the parapophysis of the centrum, and the tuberculum to the transverse process of the neural arch. In the dorsal region the parapophyses rise from the centra to the sides of the neural arches.

Among the *Theropoda* and *Sauropoda* the posterior dorsal vertebrae articulate with one another not only by zygapophyses, but by a hyposphene-hypantrum arrangement. The *hyposphene* facet is a vertical or wedge-shaped projection occurring on the posterior end of the neural arch below and continuous with the post-zygapophyses. It is received into a corresponding groove, or *hypantrum*, on the anterior face of the next vertebra behind. This arrangement is similar in function to the zygosphene-zygantrum articulation among Ophidians, except that the relative positions of pegs and sockets are interchanged. The primitive number of the sacral vertebrae seems to have been three, and additions to this number are generally made from the lumbar, sometimes from the anterior caudal series. The chevron bones of the caudals are articulated intervertebrally.

The *skull* (Fig. 472) of most Dinosaurs is small in proportion to the rest of the body, more so in *Brontosaurus*, in fact, than in any other reptile, and the brain cavity is diminutive. The latter, in proportion to the size of the head, is smaller in *Triceratops* than in any other known land vertebrate. Among the Jurassic and Cretaceous *Theropoda* and bipedal *Orthopoda* the long axis of the skull is approximately at right angles to the neck, but in the Triassic *Theropoda* and the quadrupedal *Sauropoda* and quadrupedal *Orthopoda* it more nearly continues the line of the vertebral column. The large orbits are laterally directed, and between them and the paired narial openings is frequently an antorbital vacuity, as in crocodiles, pterosaurs, and birds. The narial cavity is described by Lambe as extended into the inflated crest of the skull in the aquatic crested *Trachodontidae* (p. 398). A similar arrangement occurs in some of the existing Lamellirostrine birds.[1] There is no pineal foramen, but according to F. von Huene a rudiment of it occurs in the Triassic *Plateosaurus*. There is sometimes a little median vacuity between the parietals and supraoccipital.[2] The temporal vacuities vary considerably in form and size. The large quadrate is prominently exposed, and suturally united with the squamosal and quadrato-

[1] *Nopcsa, F.*, Palaeobiologica, vol. ii., p. 194, 1929.

[2] *Pompeckj, J. F.*, Das angebliche Vorkommen und Wandern des Parietalforamens bei Dinosauriern. Sitzb. Ges. naturf.-Freunde, Berlin, 1920, p. 109. See also *loc. cit.*, 1921, p. 1.

jugal. According to Marsh, Nopcsa, and Versluys, it seems to have been often slightly movable, as in birds. The paired premaxillae are rather

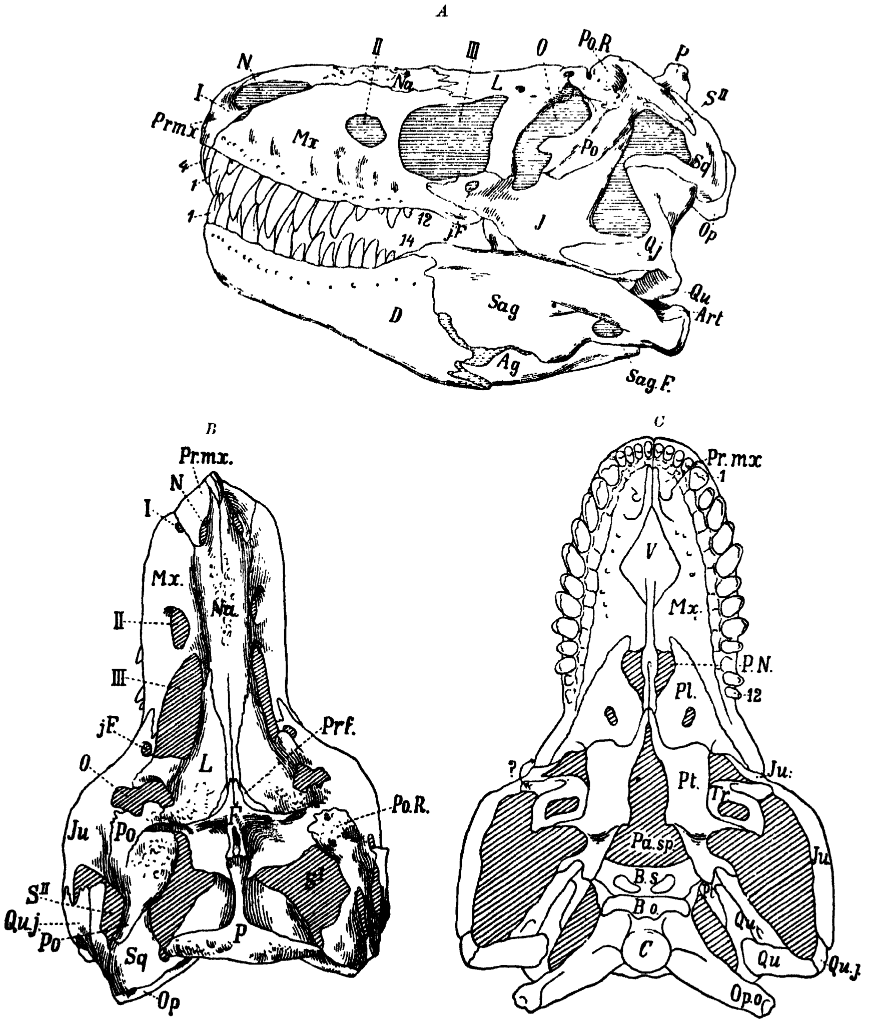


FIG. 472.

Tyrannosaurus rex Osborn. Skull and mandible in left lateral (*A*), upper (*B*), and palatal (*C*) aspects. Upper Cretaceous; Montana, U.S.A. *Ag*, angular; *Art*, articular; *Bo*, basioccipital; *Bs*, basisphenoid; *C*, occipital condyle; *D*, dentary; *F*, frontal; *I-III*, three antorbital vacuities; *jF*, jugal foramen; *Ju*, jugal; *L*, lachrymal; *Mx*, maxilla; *N*, external narial opening; *Na*, nasal; *O*, orbit; *Op.o*, opisthotic; *P*, parietal; *PN*, internal narial opening; *Pa.sp*, position of remnant of parasphenoid; *Pl*, palatine; *Po*, postorbital with a prominence (*Po.R*); *Prf*, prefrontal; *Pr.mx*, premaxilla; *Pt*, pterygoid; *Qu*, quadrate; *Qu.j*, quadrato-jugal; *S^I, II*, upper and lateral temporal vacuities; *Sag*, surangular with vacuity (*Sag.F*); *Sq*, squamosal; *Tr*, transverse (ectopterygoid), displaced or incomplete; *V*, vomer. Much reduced (after Osborn).

extensively developed, and either provided with teeth, or toothless and beak-like.

The inferior aspect of the skull is similar in a general way to that of Rhynchocephalians, except that there are no teeth on the palate. The

mandibular rami are united in a cartilaginous symphysis, and in the *Orthopoda* a toothless predentary bone is developed in front of the mandible, the sharp margin of which appears to have been sheathed in a horny beak. Teeth are confined to the margin of the jaws, and are either in deep sockets or implanted in an alveolar groove open on the inner side of the jaw.

In the *pectoral arch* clavicles and interclavicle appear to be wanting, though rudiments of these bones have been observed in some of the primitive Triassic genera.[1] The supposed occurrence of clavicles in *Psittacosaurus* lacks confirmation. The sternum is imperfectly ossified. The scapula is very strongly developed, and usually much elongated. The coracoid is flattened, with more or less rounded anterior margin, and pierced by a foramen near its articular border. Sometimes the scapula and coracoid are fused at their proximal ends, as in birds.

The bones of the appendicular skeleton are sometimes very massive, in other cases delicate and hollow; and the disparity between fore and hind quarters is often very considerable, indicating that the presacral region was ordinarily lifted from the ground. The humerus in most cases is shorter than the scapula; the radius and ulna are strongly developed, and always separate. The carpus is often incompletely ossified, and the number of metacarpals is sometimes reduced to three. The ungual phalanges are either hoofed or claw-shaped.

Many remarkably Avian characters are to be observed in the *pelvic arch* and bones of the hind limb, especially among the *Orthopoda*. The ilium is depressed and more or less extended antero-posteriorly; moderately so in the triradiate type of pelvis (*Theropoda*), very much so in the quadriradiate type (*Orthopoda*). The long ischia extend backward and downward, and usually join in a median ventral symphysis. The preacetabular process of the ilium (*spina iliaca*) which serves for the attachment of the pubis, usually extends further downward than the postacetabular or ischial process, as in birds. The acetabulum itself is open, and the sacrum is partly Avian, partly Reptilian.

In the *Theropoda* the pubes are long and slender, and fused in a ventral symphysis, which is often extended horizontally. Among the *Sauropoda* they are shorter, stouter, and broader than the ischia, directed simply downward and forward, and united distally in a median bony or cartilaginous symphysis. In the *Orthopoda* (Fig. 473) the pubis is long and broad, but does not join its fellow in the median line in front. At its base, underneath the acetabulum, it gives off a long and slender process, the *postpubis*, which is directed downward and backward parallel with the almost equally slender but somewhat longer ischium. Although this postpubic process is suggestive at first sight of the pubis of birds, it has been demonstrated by the embryological researches of Bunge[2] and Mehnert[3] that no homology between these structures exists. The Avian pelvis is in its earliest stages of development triradiate, like that of the primitive Theropodous Dinosaurs, and the pubis is directed forward as in reptiles. Later the pubis becomes secondarily shifted backwards, parallel with the ischium, and the *processus iliopectineus* must be regarded as a secondary

[1] *Huene, F. von*, Geol. u. Palaeont. Abhandl., n.f., vol. xv., p. 177, 1926.

[2] *Bunge, A.*, Zur Entwicklungsgeschichte des Beckengürtels der Amphibien, Reptilien und Vögel. Dorpat, 1880.

[3] *Mehnert, E.*, Über die Entwicklung des os pelvis der Vögel. Morphol. Jahrb., vol. xiii., p. 259, 1888.

structure peculiar to birds, with which the pubis of Dinosaurs has, of course, no homology. The postpubis of the *Orthopoda* is accordingly to be interpreted as a special or adaptive modification, probably correlated with the function of the tail in balancing the body in locomotion, or while resting on its hind quarters.[1]

The *femur* usually exceeds the humerus in length, and is placed vertical to the body, with its head extending inward into the acetabulum, as in birds. Dollo has shown that the femur of *Iguanodon*, with its large fourth trochanter (a process which is distinct from the "third trochanter" of mammals), is constructed more on the Avian than Reptilian type, and indicates a powerful caudo-femoral musculature. Still other Avian characters are exhibited by the tibia, which possesses a large cnemial crest, and is often completely embraced by the astragalus at its distal end. In the Stegosaurs these elements are fused, but in most of the carnivorous *Theropoda* the astragalus bears an ascending process, which is apposed to the anterior face of the lower end of the tibia, exactly as in Pterosaurs and young Ratite birds. The fibula is complete but often attenuated distally; the proximal tarsals are ~~two~~ in number (astragalus and calcaneum); and the distal two or three, tarsalia I-III, are usually fused into a single piece. The hind foot is tridactyl to pentadactyl, but all five metatarsals are commonly represented even when the number of functional digits is reduced.

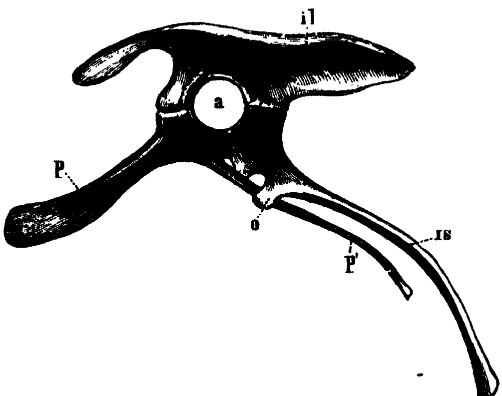


FIG. 473.
Pelvis of *Iguanodon*, $^1/_{20}$ nat. size. *a*, acetabulum; *il*, ilium; *is*, ischium; *o*, obturator process; *p*, pubis; *p'*, postpubic process.

Pebbles evidently from the stomach (gastroliths) have been found with skeletons of *Sauropoda*,[2] and eggs have been found with skeletons of both *Sauropoda* and *Orthopoda*. In structure, the egg-shell differs from that of all living reptiles, and in the thickness of the prismatic layer agrees with that of the most modern birds.[3]

Dinosaur remains were first discovered in the English Jurassic and Wealden during the early decades of the last century, and were described by Buckland

[1] In the above interpretation Zittel followed Marsh. More recently A. S. Romer has studied the probable arrangement of the muscles, and he concludes that the "postpubis" is the true pubis, "the rotation being made in relation to a change of position of the obturator muscle." He considers that "the anterior process has developed for abdominal support in the absence of an anteriorly projecting pubic ramus or a large avian sternum" (Acta Zoologica, vol. viii., p. 273, 1927). This process is named *pseudopectineal* by Nopcsa (Centralbl. f. Min., etc., 1918, p. 235).

[2] *Janensch, W.*, Ueber Magensteine bei Dinosauriern aus Deutsch-Ostafrika. Sitzb. Ges. naturf. Freunde, Berlin, 1926, p. 34.—*Wieland, G. R.*, Dinosaurian Gastroliths. Science, n.s., vol. xxiii., p. 819, 1906, and vol. xxv., p. 66, 1907.

[3] *Van Straelen, V.*, Sur les œufs fossiles du Crétacé supérieur de Rognac en Provence. Bull. Acad. Roy. Belg., Classe Sci., 1923, p. 14.—Microstructure of the Dinosaurian Egg-shells from the Cretaceous beds of Mongolia. Amer. Mus. Novit., no. 173, 1925.—Les Œufs de reptiles fossiles. Palaeobiologica, vol. i., p. 295, 1928.

in 1824 and Mantell in 1825. Owen, in 1841, established for them the order *Dinosauria*,[1] and much additional light was shed on their structure and relations by Huxley, Phillips, Marsh, and Cope prior to 1875. During subsequent years the discoveries of complete skeletons of *Iguanodon* in the Wealden of Belgium, many skeletons of primitive genera in the Triassic of Germany, and skeletons of all Mesozoic periods in North America, have provided a general knowledge of the Order. It was eventually subdivided into the three Sub-Orders of *Theropoda*, *Sauropoda*, and *Predentata* by O. C. Marsh, and also into two groups—perhaps separate Orders—*Saurischia* and *Ornithischia*, by H. G. Seeley. The *Saurischia* include the *Theropoda* and *Sauropoda*, while the *Ornithischia* correspond with the *Orthopoda* of Cope, the *Predentata* of Marsh.

A. SAURISCHIA.[2]

Reduction of dentition, when occurring, beginning at hinder end of jaws. Pubis directed forwards and downwards to meet its fellow in the middle line, without post-pubic process.

Sub-Order 1. THEROPODA.[3]

Carnivorous Dinosaurs, usually bipedal, with cutting teeth, when present, more or less laterally compressed. Brain-case incompletely ossified; antorbital vacuities large. Sclerotic plates. Mandibular ramus without coronoid process, and usually pierced by a lateral foramen in its hinder half; no predentary bone. Vertebrae and limb bones hollow, often very light, consisting of dense bone with well-formed articulations. Sternum rarely ossified. Pubes slender, with symphysis often much extended. Fore limbs shorter than the hinder pair; digits two to five in number, provided with prehensile claws; hind feet digitigrade. Abdominal ribs often present.

The *Theropoda* are carnivorous land Dinosaurs with clawed digits, and vary in size from about 25 cm. to 10 m. in length. Most of them must have walked only on their hind limbs, or possibly even leaped in kangaroo-fashion (*Hallopus*), with the forward part of the body lifted from the ground and balanced by the powerfully developed tail. The tail may have served in some cases also for swimming, as well as for a support for the animal when resting on its hind quarters and pelvic symphyses. The skeleton of many *Theropoda* is of very delicate construction.

The skull is known in few genera, and the sutures between its bones are often indistinct. All the vertebrae of the neck, except the atlas, are concave behind, but usually flattened on the anterior face of the centra; they are often longer than the dorsals, and their neural spines are only moderately developed, indicating a less powerful musculature than among the *Sauropoda*. Each sacral rib is attached to two vertebrae; the caudals bear chevron bones. Abdominal ribs have been observed in several genera.

In the pectoral arch the scapula is usually longer and stouter than the

[1] *Baur, G.*, Remarks on the Reptiles generally called Dinosauria. Amer. Naturalist, 1891, p. 434.

[2] *Huene, F. von.*, Kurze Übersicht über die Saurischia und ihre natürlichen Zusammenhänge. Palaeont. Zeitschr., vol. xi., p. 269, 1929.—*Romer, A. S.*, Pelvic Musculature of Saurischian Dinosaurs. Bull. Amer. Mus. Nat. Hist., vol. xlviii, p. 605, 1923.

[3] *Huene, F. von*, The Carnivorous Saurischia in the Jura and Cretaceous Formations principally in Europe. Revista Mus. La Plata, vol. xxix., p. 35, 1926.—Über die Dinosaurier der Aussereuropäischen Trias. Geol. u. Palaeont. Abhandl., n.f., vol. viii., p. 99, 1906.—Die Dinosaurier der Europäischen Triasformation. *Loc. cit.*, suppl. vol. i., 1907-8.

humerus, the coracoid is more or less crescentic or semicircular, and there is not always an ossified sternum. The fore limbs are smaller than the hind limbs; the carpus is, as a rule, incompletely ossified, and the clawed digits are of only moderate size. In the pelvic arch the postacetabular portion of the ilium is more elongated than the preacetabular. Both the pubic and ischial ventral symphyses are often much extended, and apparently served as a support for the body when in a crouching or sitting position. The proximal tarsals tend to form a tibio-tarsus, and in the Jurassic and Cretaceous genera the astragalus bears an ascending process, which is immovably applied against the anterior face of the tibia, as in young ostriches.

Theropoda first appear in the Trias, and become extinct in the Cretaceous; and they had an almost world-wide distribution. The Triassic forms with short, sometimes spatulate, teeth have been grouped by von Huene and Nopcsa as *Pachypodosauria*; some of the smaller and lighter forms, as *Coelurosauria*; and the more powerful and larger flesh-eaters with laterally-compressed, sabre-shaped teeth, as *Theropoda*-proper or *Megalosauria*.

Family 1. **Plateosauridae.**[1]

Large and heavy Theropoda. Teeth spatulate, constricted at base of crown. Vertebrae amphicoelous; about ten cervical vertebrae and three sacrals. Fore limb

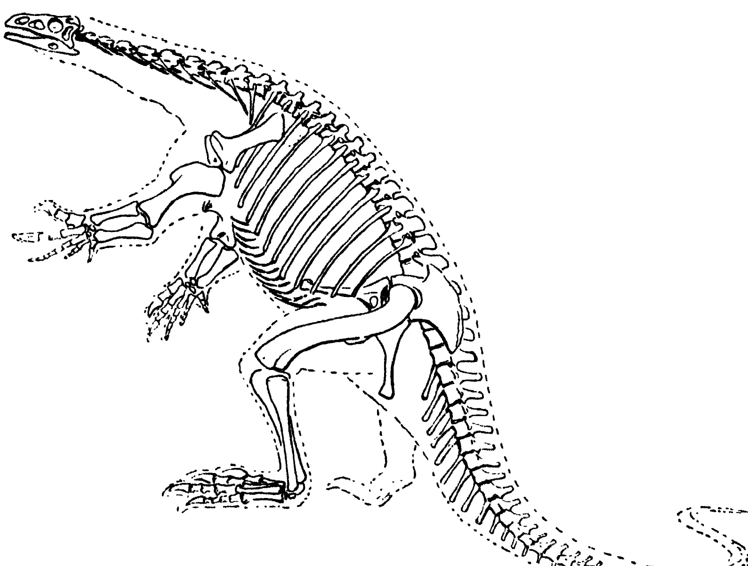


FIG. 474.

Restoration of skeleton of *Plateosaurus* by O. Jaekel, greatly reduced. Upper Triassic; Halberstadt, North Germany. The small outer toe of the hind foot is not shown. Compare with another restoration by F. von Huene, Geol. u. Palaeont. Abhandl., n.f., vol. xv., pl. vii. (xiii.), 1926, in which the hind foot is represented as digitigrade.

[1] *Broom, R., Gryponyx.* Ann. S. African Mus., vol. vii., p. 294, 1911.—*Gaudry, A., Dimodosaurus,* in Enchainements du monde animal, Foss. Second., p. 214, 1890.—*Huene, F. von,* Vollständige Osteologie eines Plateosauriden aus dem schwäbischen Keuper. Geol. u. Palaeont. Abhandl., n.f., vol. xv., p. 139, 1926.—Lebensbild des Saurischier-Vorkommens im obersten Keuper von Trossingen. Palaeobiologica, vol. i., p. 103, 1928.—*Jaekel, O., Plateosaurus.* Palaeont. Zeitschr., vol. i., p. 170, 1913.

relatively large; manus with five digits, the two outer shortened. Ilium short and deep, with long pedicle for pubis; pubis and ischium each a long narrow laminar bone, meeting its fellow along the edge in a long vertical symphysis. Femur much curved, longer than tibia; astragalus without ascending process. Hind foot with five digits, the first and fifth shortened. Well-developed abdominal ribs. Upper Triassic and Rhaetic.

Plateosaurus H. von Meyer (*Dimodosaurus* Pidancet and Chopart; *Sellosaurus* F. von Huene) (Fig. 474). One antorbital vacuity. Cervical ribs very slender. Fifteen dorsal vertebrae, only slightly amphicoelous. *P. engelhardti* H. von Meyer, about 6 m. in length. Keuper; Germany. Other species in the Keuper and Rhaetic of Germany and France, and in the Stormberg Beds of S. Africa.

Gryponyx Broom. Stormberg Beds; Orange Free State and Transvaal, South Africa.

Family 2. **Zanclodontidae.**[1]

Imperfectly known, resembling Plateosauridae, *but teeth deep, laterally compressed to two sharp edges, with the apex usually curved backwards.* Upper Triassic and Rhaetic.

Zanclodon Plieninger. Smooth teeth with edges entire or finely serrated, found with dorsal and caudal vertebrae which have high and broad neural spines. *Z. laevis* Plien. Lettenkohle; Gaildorf, Würtemberg. Other teeth in Muschelkalk. *Z. cambrensis* Newton, a dentary with teeth from Rhaetic, Bridgend, S. Wales.

Teratosaurus H. von Meyer. Maxilla indicating rather small antorbital vacuity. Three sacral vertebrae. Well-developed abdominal ribs. *T. suevicus* H. von Meyer. Stubensandstein; Heslach and Trossingen, Würtemberg.

Gresslyosaurus Rütimeyer (*Avalonia, Picrodon* Seeley; *Pachysaurus* F. von Huene). Three sacral vertebrae. Upper arm twice as long as lower arm. Femur nearly straight. Foot with reduced metatarsal v. *G. ingens* Rütim., with sacrum about 40 cm. long. Upper Keuper; near Basle. Allied species in Rhaetic of Wedmore, Somerset, and in Upper Keuper of Würtemberg.

Cladyodon Owen. Teeth from Keuper; Warwickshire.

Euskelesaurus Huxley (*Orosaurus* Huxley; *Orinosaurus* Lydekker). Stormberg Beds; Cape Province, S. Africa.

Gigantoscelus, Eucnemesaurus Van Hoepen; *Melanorosaurus* Haughton. Stormberg Beds; S. Africa.

Family 3. **Anchisauridae.**[2]

Small light Theropoda. Head small; quadrate inclined forwards and downwards; teeth short cones, laterally compressed to two sharp edges which are usually

[1] ***Huene, F. von,*** *Euskelesaurus* in Geol. u. Palaeont. Abhandl., n.f., vol. viii., p. 123, 1906.—*Zanclodon* and *Gresslyosaurus, loc. cit.*, suppl. vol. i., p. 105, 1908.—Beiträge zur Kenntnis einiger Saurischier der schwäbischen Trias [*Teratosaurus*]. Neues Jahrb. f. Min., etc., 1915, vol. i., p. 15.—***Newton, E. T.***, Megalosauroid Jaw from Rhaetic Beds near Bridgend. Quart. Journ. Geol. Soc., vol. lv., p. 89, 1899.—***Seeley, H. G.***, Large Terrestrial Saurians from the Rhaetic Beds of Wedmore Hill. Geol. Mag. [4], vol. v., p. 1, 1898.

[2] ***Broom, R.***, Dinosaurs of the Stormberg. Ann. S. African Mus., vol. vii., p. 291, 1911; also Trans. S. African Phil. Soc., vol. xvi., p. 201, 1906.—***Haughton, S. H.***, Fauna and Stratigraphy of the Stormberg Series. Ann. S. African Mus., vol. xii., p. 370, 1924.—***Hoepen, E. C. N. van***, Dinosaurs from Stormberg Beds. Ann. Transvaal Mus., vol. vii., pp. 77, 93, 1920.—***Huene,***

serrated. Vertebrae amphicoelous or amphiplatyan; neck long, with nine vertebrae; two or three sacral vertebrae. Fore limb relatively large, with five digits, the two outer shortened. Ilium expanded behind; pubis rod-shaped. Femur curved, longer than tibia; astragalus without ascending process. Hind foot with four complete digits, the fifth reduced. Triassic.

Anchisaurus Marsh (*Megadactylus* Hitchcock; *Amphisaurus* Marsh). Orbit very large and rounded; one antorbital vacuity. Vertebrae elongated. Fifth digit in hind foot reduced to a rudimentary metatarsal. *A. colurus* Marsh, about 2 m. long. Triassic; Connecticut. Other species in Massachusetts.

Ammosaurus Marsh (Fig. 475). Triassic; Connecticut.

Thecodontosaurus Riley and Stutchbury. Teeth and isolated bones. Triassic (Magnesian Conglomerate); Durdham Down, Bristol. Various fragments have been compared with this genus from Germany, N. America, S. Brazil, and South Africa; some from the German Muschelkalk probably belong to *Tanystropheus* (p. 270).

Agrosaurus Seeley. Trias; N.E. Australia.

? *Arctosaurus* Adams. Cervical vertebra from Bathurst Island, Arctic America. Perhaps Chelonian.

? *Epicampodon* Lydekker (*Ankistrodon* Huxley). Panchet Beds; Bengal, India.

Massospondylus Owen. Maleri Beds; India. Stormberg Beds; S. Africa.

Hortalotarsus Seeley; *Gyposaurus*, *Aetonyx* Broom; *Dromicosaurus*, *Aristosaurus* Van Hoepen. Stormberg Beds: S. Africa.

Fig. 475.

Ammosaurus major Marsh. Triassic; Manchester, Conn. Dorsal aspect of right hind foot. *a*, astragalus; *c*, calcaneum; *f*, fibula; *t*, tibia; t_2-t_4, distal tarsals; *I-V*, digits. 1/4 nat. size (after Marsh).

Family 4. Hallopodidae.[1]

Small leaping Theropoda. Neck comparatively short with eight to ten vertebrae; sacrum with three or four vertebrae, tail with short vertebrae in its basal portion. Fore limb very short and slender, with five short digits. Hind limb long and slender, with three or four elongated metatarsals closely apposed and similar, the first sometimes shorter, and the fifth metatarsal much reduced. Astragalus without ascending process. Calcaneum with a prominent tuber. Abdominal ribs. No dermal armour. Upper Triassic.

Hallopus Marsh. Three sacral vertebrae. Femur nearly as long as tibia.

F. von, Nachträge zu meinen früheren Beschreibungen von triassischer Saurischia. Geol. u. Palaeont. Abhandl., n.f., vol. xiii., p. 69, 1914.—*Marsh, O. C.*, Notes on Triassic Dinosauria. Amer. Journ. Sci., vol. xliii., p. 543, 1892.—*Seeley, H. G.*, *Agrosaurus macgillivrayi*. Quart. Journ. Geol. Soc., vol. xlvii., p. 164, 1891.—*Massospondylus*. Ann. Mag. Nat. Hist. [6], vol. xv., p. 102, 1895.—*Thecodontosaurus* and *Palaeosaurus*. *Loc. cit.*, p. 144, 1895.

[1] *Fraas, E.*, Die neuesten Dinosaurierfunde in Württemberg. Jahresh. Ver. vaterl. Naturk. Württ., vol. lxx., p. 60, 1914.—*Huene, F. von*, and *Lull, R. S.*, *Hallopus victor* Marsh. Amer. Journ. Sci., vol. xxv., p. 113, 1908.—*Huene, F. von*, Beiträge zur Geschichte der Archosaurier. Geol. u. Palaeont. Abhandl., n.f., vol. xiii., p. 3, 1914.—*Procompsognathus triassicus* E. Fraas. Acta Zoologica, vol. ii., p. 360, 1921.—*Woodward, A. S.*, New Dinosaurian Reptile (*Scleromochlus taylori*, gen. et sp. nov.). Quart. Journ. Geol. Soc., vol. lxiii., p. 140, 1907.

First digit of foot complete but short; fifth metatarsal without phalanges.

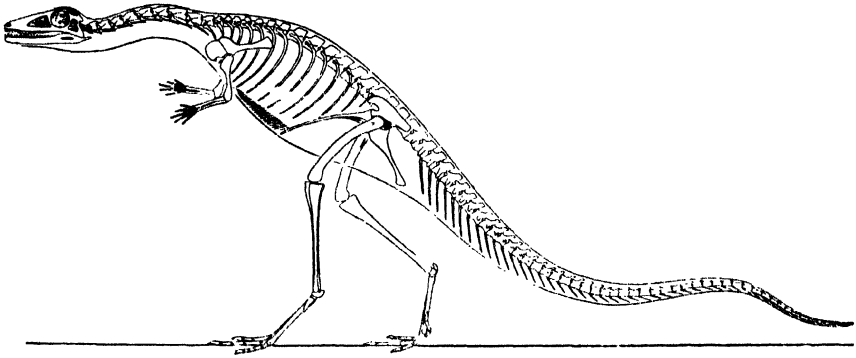


FIG. 476.
Procompsognathus triassicus E. Fraas. Restoration of skeleton by F. von Huene, about 1/8 nat. size. Middle Keuper; Würtemberg.

H. victor Marsh, a fragmentary skeleton without skull, from Upper Triassic near Canyon City, Colorado.

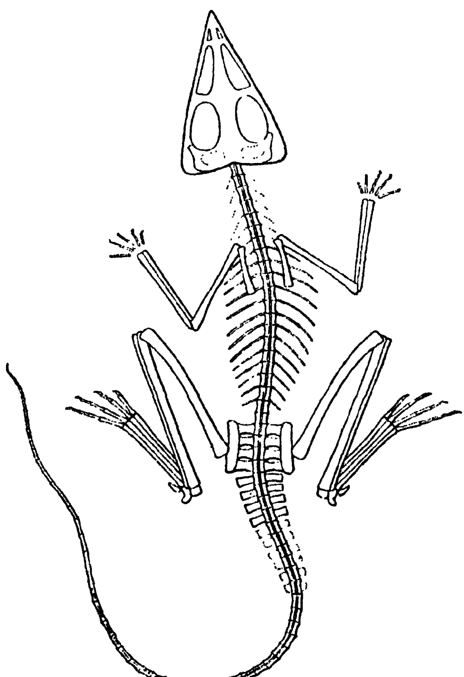


FIG. 477.
Scleromochlus taylori A. S. Woodward. Restoration of skeleton by A. S. Woodward, 2/3 nat. size. Upper Triassic; Lossiemouth, Scotland.

Procompsognathus E. Fraas (Fig. 476). Skull elongated, with very large round orbit and triangular antorbital vacuity. Teeth slightly recurved. About fourteen dorsal vertebrae, and probably three sacrals. Hind limb more than three times as long as fore limb. *P. triassicus* E. Fraas, with skull about 8 cm. long, from Middle Keuper of Pfaffenhofen, Würtemberg.

Pterospondylus Jaekel. Upper Keuper; Halberstadt.

Scleromochlus A. S. Woodward (Fig. 477). Teeth very small. About eight cervical, thirteen dorsal, four sacral vertebrae, and more than fifty caudals. Hind limb more than twice as long as fore limb. Femur nearly as long as tibia; the four complete metatarsals of equal length; fifth metatarsal a mere rudiment. Shape of coracoid unknown. No clavicular arch. Acetabulum apparently perforate. *S. taylori* A. S. Woodw., known by skeletons from 20 to 25 cm. in length, from Upper Triassic, Lossiemouth, Elgin, Scotland.

Family 5. **Podokesauridae.**[1]

Small leaping Theropoda. Trunk short, with elongated vertebrae. Tail very long, with much elongated vertebrae. Triassic.

Podokesaurus Talbot. Slender cervical ribs. About eleven dorsal vertebrae. Tail more than 1½ times the rest of the skeleton. *P. holyokensis* Talbot, about a metre long, known by part of skeleton without skull, from Upper Triassic, Mount Holyoke, Massachusetts.

? *Coelophysis* Cope. Upper Triassic; New Mexico.

Saltopus F. von Huene. About fourteen dorsal vertebrae, and four sacrals. Femur much curved, shorter than tibia. Metatarsus more than two-thirds as long as tibia. *S. elginensis* F. von Huene, known by part of skeleton without skull, from Upper Triassic, Elgin, Scotland.

Family 6. **Compsognathidae.**[2]

Cervical vertebrae slightly opisthocoelous, postcervicals amphiplatyan. Neck long and flexible; cervical ribs styliform. Pubes stout, ischia shorter and more slender. Femur shorter than tibia; astragalus with ascending process. Metatarsals long; manus and pes with three functional digits, the inner and outer digits rudimentary. Upper Jurassic.

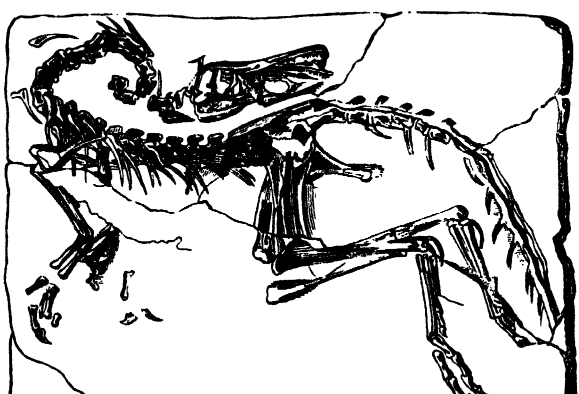


Fig. 478.
Compsognathus longipes Wagner. Lithographic Stone; Kelheim, Bavaria. 1/4 nat. size (after A. Wagner).

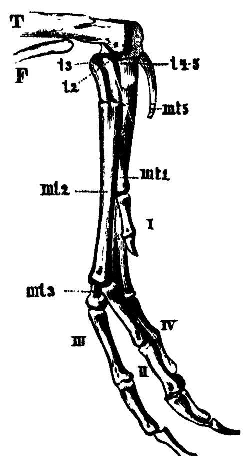


Fig. 479.
Compsognathus longipes Wagner. Left hind foot. *F*, fibula; *mt*, metatarsals; *T*, tibia; t^2-t^5, distal tarsals. Nat. size (after Baur).

Compsognathus Wagner (Figs. 478, 479). Represented by a unique skeleton from the Lithographic Stone of Kelheim, Bavaria, in the Munich Museum.

[1] *Huene, F. von*, Ein primitiver Dinosaurier aus dem mittleren Trias von Elgin [*Saltopus*]. Geol. u. Palaeont. Abhandl., n.f., vol. viii., p. 317, 1910.—Revision von *Podokesaurus holyokensis* M. Talbot. *Loc. cit.*, vol. xiii., p. 31, 1914.—*Coelophysis*. Bull. Amer. Mus. Nat. Hist., vol. xxxiv., p. 500, 1915.—*Talbot, M.*, *Podokesaurus holyokensis*. Amer. Journ. Sci., vol. xxxi., p. 469, 1911.

[2] *Huene, F. von*, Der vermuthliche Hautpanzer des *Compsognathus longipes* Wagn. Neues Jahrb. f. Min., etc., 1901, vol. i., p. 157.—Eine neue Rekonstruktion von *Compsognathus*. Centralbl. f. Min., etc., 1925, Abt. B, p. 157.—*Nopcsa, F.*, Neues über *Compsognathus*. Neues Jahrb. f. Min., etc., Beil.-Bd. xvi., p. 476, 1903.—*Wagner, A.*, *Compsognathus*. Abh. k. bay. Akad. Wiss., math.-phys. Cl., vol. ix., p. 94, 1864.

In the body cavity it contains a small skeleton, which is interpreted by Marsh as an embryo, by Nopcsa as a reptile swallowed for food. Skull about 7·5 cm. long, its long axis at right angles to the relatively long neck. The ten cervical and thirteen dorsal vertebrae have a combined length of 20 cm., and the caudals, of which only fifteen are preserved, measure about the same. There are five sacral vertebrae. Fore limbs only half as long as the hinder pair. Proximal tarsals tend to form with the tibia a bird-like tibio-tarsus; distal tarsals represented by three small flattened bones. The supposed epidermal scales are probably only rock structures. *C. longipes* Wagner.

Kouphichnium Nopcsa. Footprint from Lithographic Stone, Solenhofen.

Family 7. **Coeluridae.**[1]

Small and slender Theropoda. Skull small, teeth small, and lower jaw short and deep; quadrate vertical or inclined forwards and downwards. Neck long and slender. Fore limb long and slender. Ilium long and low, curved down in front. Femur shorter than tibia, and foot with three complete digits, the middle metatarsal not reduced at the proximal end. Upper Triassic to Upper Cretaceous.

Halticosaurus F. von Huene. Keuper; Germany.

Coelurus Marsh. Known only by portions of the vertebral column, pelvis, and limb bones. Centra, neural arches, and all processes of the vertebrae have hollow interiors, and the neural arches are suturally united with their centra. In the cervical and trunk regions the neural canal is greatly dilated. Upper Jurassic; Wyoming and Maryland.

Ornitholestes Osborn. Skull with two pairs of antorbital vacuities; frontal bones firmly united with the parietals. About twenty-three presacral vertebrae, four sacrals. Hand much elongated, with first digit divergent and two outer digits reduced. Pelvic bones united. Perhaps identical with *Coelurus*. *O. hermanni* Osborn, known by nearly complete skeleton about 2 m. in length, from Upper Jurassic (Morrison Formation), Wyoming.

Brasileosaurus F. von Huene. Lower Cretaceous; State of San Paulo, Brazil.

Thecospondylus Seeley; *Thecocoelurus* F. von Huene; *Calamospondylus* Lydekker. Wealden; England. *Tichosteus* Cope. Upper Jurassic; Colorado. Detached vertebrae.

Aristosuchus Seeley. Wealden; Isle of Wight.

Elaphrosaurus Janensch. Tendaguru Beds; Tanganyika Territory.

Velociraptor, *Saurornithoides* Osborn. Upper Cretaceous (Djadochta Beds); Mongolia.

Chirostenotes Gilmore. Manus and perhaps slender lower jaw from Upper Cretaceous (Belly River Beds), Red Deer River, Alberta, Canada.

[1] *Gilmore, C. W.*, New Coelurid Dinosaur from the Belly River Cretaceous of Alberta [*Chirostenotes*]. Canada Geol. Surv., Bull. no. 38, p. 1, 1924.—*Janensch, W.*, Die Coelurosaurier und Theropoden der Tendaguru-Schichten. Palaeontographica, suppl. vii., 1st ser. i., p. 1, 1925.—Reconstruirtes Skelett von *Elaphrosaurus*. *Loc. cit.*, p. 279, 1929.—*Osborn, H. F.*, Restudy of *Ornitholestes hermanni*. Bull. Amer. Mus. Nat. Hist.. vol. xxxv., p. 735, 1917.—Three new *Theropoda*, *Protoceratops* Zone, Central Mongolia. Amer. Mus. Novit., no. 144, 1924.—*Seeley, H. G.*, *Aristosuchus pusillus* (Owen). Quart. Journ. Geol. Soc., vol. xliii., p. 221, 1887.

Family 8. **Megalosauridae.**[1]

Large and heavy Theropoda, with large skull in which the suture between the frontals and parietals is loose. Quadrate inclined backwards and downwards, and lower jaw long; teeth deep, laterally compressed to two sharp edges which are usually serrated, and the apex usually curved backwards. Neck stout, with short opisthocoelous vertebrae. Fore limb small, with five digits of which the two outer are short; claws relatively large, strongly curved. Ilium expanded in front, with large pedicle for pubis; pubis and ischium expanded at distal end. Femur longer than tibia: astragalus with ascending process; metatarsals II *to* IV *subequal, not compressed, bearing three functional digits, metatarsal* I *reduced and bearing small retroverted digit; metatarsal* V *rudimentary.* Jurassic and Wealden.

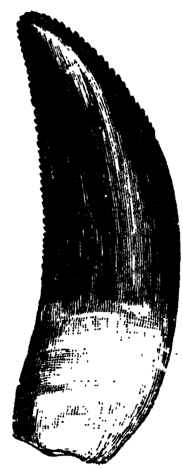


FIG. 480.
Megalosaurus bucklandi H. v. Meyer. Tooth. Bathonian; Stonesfield, England. Nat. size.

Megalosaurus Buckland (*Poikilopleuron* Deslongchamps; *Streptospondylus* H. von Meyer; *Proceratosaurus* F. von Huene) (Fig. 480). Laterally compressed bony horn core observed on nasal bones of one small species, *M. bradleyi* A. S. Woodward. Four teeth in premaxilla. One large antorbital vacuity. Five sacral vertebrae. Bones of pelvis and of metatarsus not united. *M. bucklandi* H. von Meyer, with scapula 80 cm. and femur 1 m. long, known by portions of jaws and isolated bones from the Lower Oolites of Oxfordshire, Wiltshire, and Dorset; the first Dinosaur discovered. *M.* (*Proceratosaurus*) *bradleyi* A. S. Woodward, known by skull 26 cm. in length, from Great Oolite, Gloucestershire. *M.* (*Streptospondylus*) *cuvieri* Owen. Oxford Clay; Oxfordshire, and Honfleur, N. France.

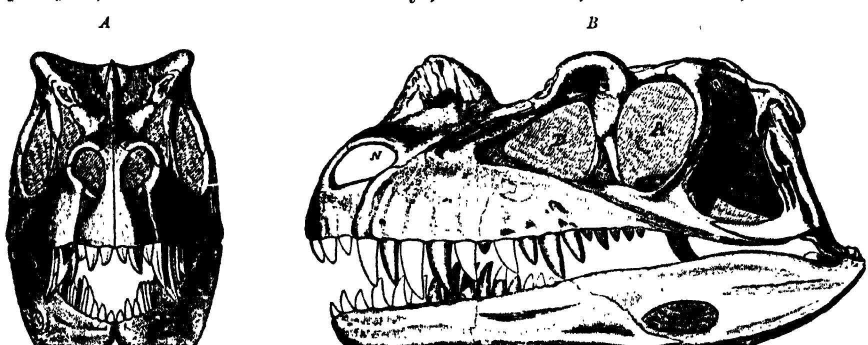


FIG. 481.
Ceratosaurus nasicornis Marsh. Skull and mandible from anterior (*A*) and lateral (*B*) aspects. Upper Jurassic; Colorado. *A*, orbit; *D*, antorbital vacuity; *D'*, mandibular vacuity; *N*, external nostril; *S*, lateral temporal vacuity. $^1/_8$ nat. size (after Marsh).

Various teeth and fragments much resembling those of *Megalosaurus* are known from the Cretaceous of Madagascar, Tanganyika Territory, India,

[1] *Andrews, C. W.*, Theropodous Dinosaur from Lower Lias of Barrow-on-Soar. Ann. Mag. Nat. Hist. [9], vol. viii., p. 570, 1921.—*Gilmore, C. W.*, Osteology of the Carnivorous Dinosauria in the U.S. National Museum. U.S. Nat. Mus., Bull. 110, 1920.—Fore limb of *Allosaurus fragilis.* Proc. U.S. Nat. Mus., vol. xlix., p. 501, 1915.—*Hay, O. P.*, Skull of *Ceratosaurus.* Proc. U.S.

Australia, and South America, but these probably belong to other genera. An ungual phalange is also known from the Jurassic of Cape Patterson, Victoria, Australia, a footprint from N.E. Greenland.

Altispinax F. von Huene. Middle dorsal vertebrae with very high neural spines. *A. dunkeri* Koken sp., with height of these neural spines equalling length of four vertebral centra. European Wealden.

Ceratosaurus Marsh (Figs. 481, 482). Laterally compressed bony horn core on nasal bones. Three teeth in premaxilla. Five sacral vertebrae. Fore limbs very small. Ilium comparatively long and low. Pelvic bones united, and three metatarsals united. Small bony dermal scutes in median longitudinal row on back, also a few others. *C. nasicornis* Marsh, known by greater part of skeleton about 5 to 6 m. in length. Upper Jurassic; Colorado.

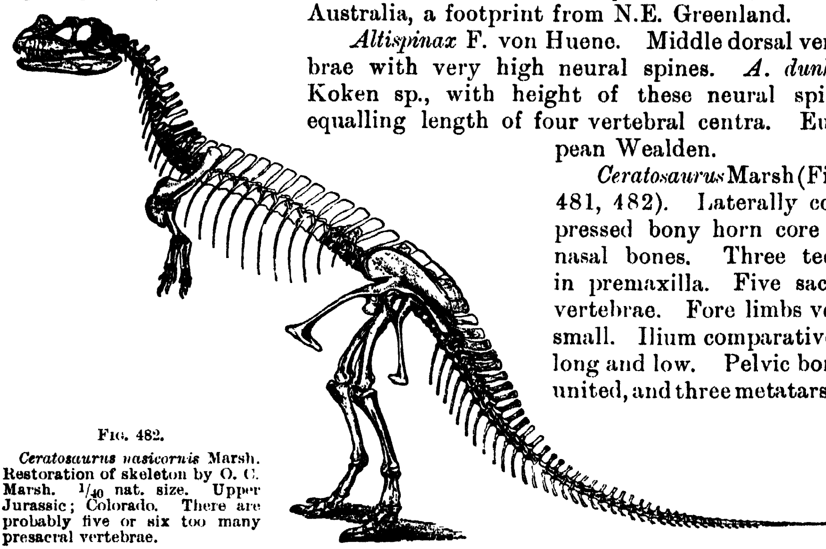


FIG. 482.
Ceratosaurus nasicornis Marsh. Restoration of skeleton by O. C. Marsh. $^1/_{40}$ nat. size. Upper Jurassic; Colorado. There are probably five or six too many presacral vertebrae.

Allosaurus Marsh (*Creosaurus* Marsh; ? *Antrodemus* Leidy) (Fig. 483). No nasal horn core. Five teeth in premaxilla. A small second antorbital vacuity near narial opening. Digits IV, V of manus much reduced. Pelvic bones and metatarsal bones not united. *A. fragilis* Marsh, known by nearly complete skeleton about 5 m. in length. Upper Jurassic; Colorado and Wyoming. Other species perhaps in Tendaguru Beds, Tanganyika Territory, Africa.

Sarcosaurus Andrews. Small pelvis, etc. Lower Lias; England.

Nuthetes Owen. Very small, supposed to have conical dermal bones. Purbeck Beds; Swanage.

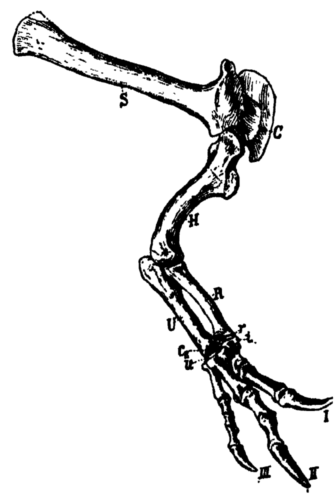


FIG. 483.
Allosaurus fragilis Marsh. Right fore limb. Upper Jurassic; Colorado. *C*, coracoid; *H*, humerus; *R*, radius; *S*, scapula; *U*, ulna; c_2, centrale 2; *i*, intermedium; *r*, radiale; *u*, space for ulnare. *I-III*, digits 1-3. $^1/_{16}$ nat. size (after Gilmore).

Nat. Mus., vol. xxxv., p. 359, 1908.—*Huene, F. von*, Reptiles of the Order *Saurischia* from England and France. Ann. Mag. Nat. Hist. [9], vol. xvii., p. 473, 1926.—*Megalosaurus*. Revista Mus. La Plata, vol. xxix., p. 45, 1926.—*Nopcsa, F.*, Genus *Streptospondylus*. Beitr. Palaeont. u. Geol. Österr.-Ungarns, vol. xix., p. 59, 1906; also Geol. Mag. [5], vol. ii., p. 289, 1905.—*Osborn, H. F.*, Skull of *Creosaurus*. Bull. Amer. Mus. Nat. Hist., vol. xix., p. 697, 1903.—Cranium of *Allosaurus*. Mem. Amer. Mus. Nat. Hist., n.s., vol. i., p. 27, 1912.—*Phillips, J.*, Geology of Oxford, p. 523, 1871.—*Woodward, A. S.*, Skull of *Megalosaurus* from Great Oolite. Quart. Journ. Geol. Soc., vol. lxvi., p. 111, 1910.

Family 9. **Dinodontidae.**[1]

Very large and heavy Theropoda, with large skull in which the frontals and parietals are firmly united. Quadrate long and nearly vertical, and lower jaw deep. Large sabre-shaped teeth. Cervical vertebrae opisthocoelous, very short and wide. Ilium long, extended far forwards and decurved, with very short pedicle for pubis. Fore limb very small and manus much reduced. Femur about as long as tibia; astragalus with ascending process; metatarsals of three digits crowded together; small first digit of foot reverted. Cretaceous.

Dinodon Leidy (*Aublysodon* Cope). Teeth from Upper Cretaceous, Judith River, Montana. Generally regarded as belonging to one of the following genera.

Tyrannosaurus Osborn (*Dynamosaurus* Osborn; *? Manospondylus* Cope) (Fig. 472). Skull very deep and laterally compressed; four small teeth in premaxilla. Nine or ten cervical, thirteen or fourteen dorsal, and five sacral vertebrae. Small reduced manus imperfectly known. Pelvic bones united; pubis with very large distal expansion; ischium short, tapering distally. Well-developed abdominal ribs and some dermal plates. *T. rex* Osborn, 10 m. in length. Upper Cretaceous (Lance); Montana, perhaps also Dakota.

Gorgosaurus Lambe (*Albertosaurus* Osborn). Skull less deep than in *Tyrannosaurus*; four small teeth in premaxilla. Humerus about one-quarter as long as femur; manus with only first and second digits complete. Pelvic bones not united. Rudiment of metatarsal V in hind foot. *G. libratus* Lambe, with skeleton about 9 m. long. Upper Cretaceous (Belly River); Red Deer River, Alberta, Canada. Supposed by Lambe to show a paired ossification of the sternum. Other species in the Edmonton Formation, Alberta (*Albertosaurus*).

Dromaeosaurus Matthew and Brown. Three large teeth in premaxilla. Belly River Formation; Alberta. Judith River Formation; Montana.

Dryptosaurus Marsh (*Laelaps* Cope). Cretaceous; New Jersey.

Erectopus F. von Huene. Gault; N. France.

Carcharodontosaurus Stromer. Lower Cenomanian; near Gebel Harra, Egypt.

Genyodectes A. S. Woodward (*? Loncosaurus* Ameghino). Upper Cretaceous; Neuquen, Argentina. *Orthogoniosaurus* Gupta. Lameta Beds; India.

Fragments of undetermined genera in the Cretaceous of the Sahara, Madagascar, India, and New South Wales (Australia).

Family 10. **Spinosauridae.**[1]

Gigantic Theropoda. Teeth not much curved. All presacral vertebrae opisthocoelous, the neural spines of the dorsals extremely long. Upper Cretaceous.

[1] *Abel, O.*, Plastische Rekonstruktion des Lebensbildes von *Tyrannosaurus rex* Osborn. Palaeobiologica, vol. iii., p. 103, 1930—*Lambe, L. M.*, Lower Jaw of *Dryptosaurus incrassatus* (Cope). Ottawa Naturalist, vol. xvii., p. 133, 1903.—Cretaceous Theropodous Dinosaur *Gorgosaurus*. Canada Geol. Surv., Mem. 100, 1917.—*Matthew, W. D.*, and *Brown, B.*, Family *Deinodontidae*. Bull. Amer. Mus. Nat. Hist., vol. xlvi., p. 367, 1922.—*Deinodontidae* from the Cretaceous of Alberta. Amer. Mus. Novit., no. 89, 1923.—*Osborn, H. F.*, *Tyrannosaurus* and other Cretaceous Carnivorous Dinosaurs. Bull. Amer. Mus. Nat. Hist., vol. xxi., p. 259, 1905; also *loc. cit.*, vol. xxii., p. 281, 1906, and vol. xxxv., p. 761, 1916.—Crania of *Tyrannosaurus* and *Allosaurus*. Mem. Amer. Mus. Nat. Hist., n.s., vol. i., p. 3, 1912.—*Parks, W. A.*, *Albertosaurus arctunguis*. Univ. Toronto Studies, Geol. Ser., no. 25, 1928.—*Stromer, E.*, Ein Skelett-Rest von *Carcharodontosaurus* nov. gen. Abhandl. Bay. Akad. Wiss., math.-naturwiss. Abt., n.f., no. 9, 1931.

[1] *Stromer, E. von*, *Spinosaurus aegyptiacus* n. gen. und n. sp. Abhandl. k. bay. Akad. Wiss., math.-naturw. Kl., vol. xxviii., p. 32, 1915.

Spinosaurus E. von Stromer. Some neural spines 1·80 m. in length. Cenomanian ; Egypt.

Family 11. **Ornithomimidae.**[1]

Very slender Theropoda. Skull small, teeth reduced or absent, and quadrate inclined forwards and downwards. Long axis of skull at right angles to that of long slender neck. Fore limb long, with three subequal digits. Ilium long and low, curved down in front. Femur shorter than tibia ; astragalus with ascending process ; foot elongated with three crowded digits, the middle metatarsal attenuated at the proximal end. Cretaceous.

Ornithomimus Marsh. Known by hind foot and fragments from near Denver, Colorado. Fifth metatarsal absent. Other fragments from Judith River Formation, Montana.

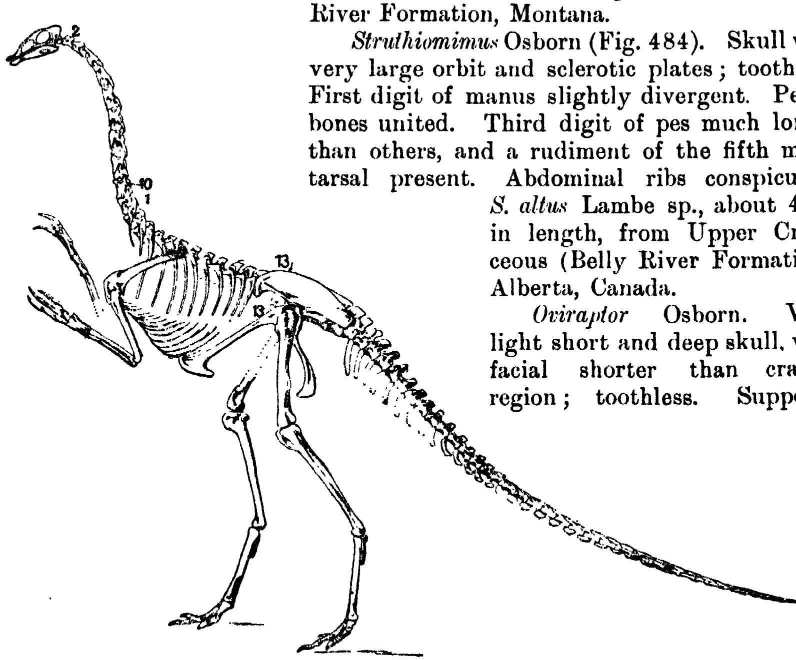


FIG. 484.
Struthiomimus altus Lambe sp. Restoration of skeleton by Osborn, 1/30 nat. size. Upper Cretaceous ; Alberta, Canada.

Struthiomimus Osborn (Fig. 484). Skull with very large orbit and sclerotic plates ; toothless. First digit of manus slightly divergent. Pelvic bones united. Third digit of pes much longer than others, and a rudiment of the fifth metatarsal present. Abdominal ribs conspicuous. *S. altus* Lambe sp., about 4 m. in length, from Upper Cretaceous (Belly River Formation), Alberta, Canada.

Oviraptor Osborn. Very light short and deep skull, with facial shorter than cranial region ; toothless. Supposed to possess T-shaped interclavicle. *O. philoceratops* Osborn, found on nest of Ceratopsian eggs. Upper Cretaceous (Djadochta Beds) ; Mongolia.

Coelosaurus Leidy. New Jersey and Maryland.

? *Labrosaurus* Marsh. Jaw partly toothed. Morrison Beds ; Colorado.

[1] *Lambe, L. M.*, Manus of *Ornithomimus*. Ottawa Naturalist, vol. xviii., p. 33, 1904.—Fore limb. *Loc. cit.*, vol. xxvii., p. 129, 1914.—*Nopcsa, F.*, Probable Habits of *Struthiomimus*. Ann. Mag. Nat. Hist. [9], vol. x., p. 152, 1922.—*Osborn, H. F.*, Skeletal Adaptations of *Ornitholestes*, *Struthiomimus*, etc. Bull. Amer. Mus. Nat. Hist., vol. xxxv., p. 733, 1917.—*Oviraptor philoceratops*. Amer. Mus. Novit., no. 144, p. 7, 1924.—*Parks. W. A.*, *Struthiomimus samueli*. Univ. Toronto Studies, Geol. Ser., no. 26, 1928.—*S. brevetertius*. Trans. Roy. Soc. Canada [3], vol. xx., sect. iv., p. 65, 1926.—*Sternberg, C. M.*, Canadian Field-Naturalist, vol. xlvi., p. 99, 1932.

According to F. von Huene, the femur named *Megalosaurus bredai* Seeley, from the Maastricht Chalk, Holland, and the claw named *M. lonzeensis* Dollo, from the Lower Senonian near Namur, Belgium, probably belong to *Ornithomimidae.* The family also seems to be represented in the Cretaceous of Lake Tchad, West Africa; in the Upper Cretaceous (Lameta Beds) of Jubbulpore, India; and in the Upper Cretaceous of Patagonia (*Clasmodosaurus* Ameghino).

Sub-Order 2. SAUROPODA.[1] (*Cetiosauria.*)

More or less massive, herbivorous or omnivorous, quadrupedal Dinosaurs, with long neck, long tail, and short trunk. Skull relatively small; brain-case completely ossified; antorbital vacuity large. Mandibular ramus without coronoid process; no predentary bone. Teeth spatulate, with anterior and posterior cutting edges. Cervical and anterior dorsal vertebrae opisthocoelous and much hollowed on each side; the rest amphiplatyan or slightly amphicoelous. Neural canal much expanded in the sacrum. Sternum ossified. Pubes moderately long, broad, and united distally by cartilage; ischia also broad and similarly meeting distally. Limb bones solid, femur without prominent inner or fourth trochanter. Fore limbs never more than slightly shorter than the hinder pair. All four feet semiplantigrade, with five digits, of which the outer two are more or less reduced; distal row of carpals and tarsals apparently unossified. Dermal armour absent.

The *Sauropoda* exhibit more resemblances to *Crocodilia* than the other Sub-Orders of Dinosaurs, and it is not surprising that the first fragmentary remains of *Cetiosaurus* were referred by Owen to a supposed Crocodilian of an extinct Sub-Order which he named *Opisthocoelia.* These Dinosaurs may have arisen from a primitive group nearly similar to that of the Triassic *Plateosauridae* (p. 375), which connects them with the *Theropoda.* They include the largest land animals known, some of them having attained a length of 30 m. or more. The relatively large size of their fore limbs and the shape of their fore feet show that they were quadrupedal; and their dentition suggests that they fed on succulent plants, probably water plants, and the animal life associated with them. Their remains are found in both estuarine and marine deposits, and they evidently frequented swamps, spending much of their life in water. The late Prof. E. D. Cope suggested that their long neck enabled them to reach the surface to breathe when they were walking on the bottom and feeding in water of considerable depth.

The skull is incompletely known except in the genera *Diplodocus*, *Morosaurus*, *Brontosaurus*, and *Helopus.* Long cylindrical or spatulate teeth, with anterior and posterior cutting edges, are present in the paired premaxillae and in at least the anterior portion of the maxillae. The orbits are large and laterally directed, and the antorbital vacuities are also extensive. The external nares are either paired and placed laterally (*Morosaurus*), or single and situated at the apex of the skull (*Diplodocus*).

The cervical and anterior dorsal vertebrae are opisthocoelous, and much

[1] *Huene, F. von*, Grundlagen der jetztigen Kenntnis der Sauropoden. Eclogae geol. Helvetiae, vol. xx., p. 444, 1927.—Review of present Knowledge of the Sauropoda. Mem. Queensland Mus., vol. ix., p. 121, 1927.—*Janensch, W.*, Sauropoden der Tendaguru-Expedition. Palaeontographica, suppl. vii., 1st ser. ii., p. 1, 1929.—*Nopcsa, F.*, Zur Systematik und Biologie der Sauropoden. Palaeobiologica, vol. iii., p. 40, 1930.—*Versluys, J.*, Waren die sauropoden Dinosaurier Pflanzenfresser? Zool. Jahrb., Abt. f. Systematik, etc., vol. xxix., p. 425, 1910.

hollowed along the sides. The double-headed cervical ribs are fused in part at least with their respective centra and neural arches, and the neural spines are sometimes reduced and paired, as in *Diplodocus*. In the posterior dorsal vertebrae there is a hyposphene-hypantrum arrangement, in addition to the pre- and post-zygapophyses. The centra of the dorsal vertebrae (Fig. 485), and sometimes also of the other regions, contain large internal cavities, which were probably pneumatic during life. These chambers, of which there are one or more on each side, are separated by a median longitudinal septum, not always continuous, and open outwardly by a foramen or elongated aperture near the base of the neural arch. In the presacral and anterior caudal vertebrae, the neural arches and spines are likewise hollowed or buttressed. Each sacral vertebra supports its own rib. The neural arches of the three primitive sacral vertebrae are usually fused together, while those of the vertebrae added in front and behind are separate. The neural canal in the sacrum is expanded to twice or three times the diameter of the brain cavity.[1] The posterior caudals have solid centra, often slightly concave behind, and flat or more rarely concave in front. Chevron bones are well developed, Y-shaped near the base of the tail, and gradually passing backwards in a pair of horizontally extended bars. A lash of rod-shaped vertebrae with conical ends sometimes occurs at the end of the tail.

The limb bones are almost or completely solid, and their rough extremities show that the articulations were completed with much cartilage. In the pectoral arch the scapula is elongated, and much more expanded proximally than at its distal end. The coracoid is small, more or less rounded anteriorly, and suggestive of the corresponding element in Rhynchocephalians. There is a pair of sternal bones. The humerus has a distinct head, and is somewhat Crocodilian. The pelvic bones are never coössified. The ilium exhibits only a slight preacetabular extension, and the broad ischium is without an obturator process. The pubes are stout, directed downwards and forwards, and meet in a cartilaginous symphysis. The femur is considerably longer than the tibia and fibula, and its large head is directed inward from the shaft to enter the acetabulum. The astragalus is without an ascending process. All the phalanges are short, and the ungual phalanges of the three inner digits are compressed claws originally sheathed with horn. One footprint is known from the Morrison Beds of Colorado.

Remains of *Sauropoda* occur principally in the Middle and Upper Jurassic and Wealden of England and Northern France, and in the equivalent formations of the western United States, especially Wyoming and Colorado. They are also known from the Jurassic of Queensland, Australia. They are especially abundant in Tanganyika Territory (East Africa), Madagascar, India, China, Brazil, and Patagonia. The latest from the uppermost Cretaceous in Patagonia are associated with primitive Mammals.

The determination of the genera and species in the *Sauropoda* is especially difficult on account of the large size of the fragmentary specimens, the lack of knowledge of changes which occur during growth, and the uncertainty as to which individuals are adult.[2] The nomenclature has also been compli-

[1] *Lull, R. S.*, Functions of the "Sacral Brain" in Dinosaurs. Amer. Journ. Sci., vol. xliv., p. 471, 1917.

[2] *Mook, C. C.*, Criteria for the Determination of Species in the *Sauropoda*. Bull. Amer. Mus. Nat. Hist., vol. xxxvii., p. 355, 1917.

cated, as in other groups of Dinosaurs, by various attempts to replace definite names by others given to indeterminable fragments.

Family 1. **Cetiosauridae.**[1]

Teeth broad spatulate, constricted at base. Neural spines of vertebrae simple; presacral vertebrae slightly opisthocoelous; caudal vertebrae amphiplatyan or amphicoelous, except in terminal lash where they have conical ends. Fore leg shorter than hind leg; long metacarpals, short metatarsals. Pubis very broad throughout; ischium less broad, meeting its fellow distally side to side. Jurassic.

Cetiosaurus Owen (*Cardiodon* Owen; *Cetiosauriscus* F. von Huene). Brain case much resembling that of *Plateosaurus.*[2] Bone of vertebral centra very finely cancellated (spongy). Lateral pits in dorsal vertebrae very shallow; five or six fused sacral vertebrae. Sternum paired as usual in *Sauropoda. C. oxoniensis* Phillips, with proportions of length of humerus to that of femur, 77 : 100; length of tibia to that of femur, 58 : 100. Length of femur, 1·65 m. Great Oolite; Oxford. *C.* (*Cetiosauriscus*) *leedsi* Hulke sp., with proportions of length of humerus to that of femur, 69 : 100. Length of femur, 1·36 m. Terminal lash of tail found. Oxford Clay; Peterborough. *C.* (*Cetiosauriscus*) *greppini* F. von Huene. Kimmeridgian; Moutier, Switzerland.

Dystrophaeus Cope. Jurassic; Painted Canyon, Utah, U.S.A.

Haplocanthosaurus Hatcher. Bone of vertebral centra more coarsely cancellated than in *Cetiosaurus. H. priscus* and *H. utterbacki* Hatcher. Upper Jurassic (Morrison Formation); Oil Creek, Canyon City, Colorado.

Elosaurus Peterson and Gilmore. Upper Jurassic (Morrison Formation); Wyoming. Known only by remains of immature individuals.

Family 2. **Brachiosauridae.**[3]

As Cetiosauridae, *but vertebrae more cavernous; neural spines more buttressed, and fore limb comparatively slender, as long as, or longer than the hind limb.* Jurassic and Cretaceous.

Brachiosaurus Riggs. Neural spines decrease in length from mid-dorsal

[1] *Hatcher, J. B.*, Osteology of *Haplocanthosaurus.* Mem. Carnegie Mus., vol. ii., no. 1, 1903. —*Huene, F. von, Dystrophaeus viaemalae* Cope in neuer Beleuchtung. Neues Jahrb. f. Min., etc., Beil.-Bd. xix., p. 319, 1904.—Über einen Sauropoden im obern Malm des Berner Jura. Eclogae geol. Helvetiae, vol. xvii., p. 80, 1922; also *loc. cit.*, vol. xx., p. 445, 1927.—*Peterson, O. A.*, and *Gilmore, C. W.*, *Elosaurus.* Ann. Carnegie Mus., vol. i., p. 490, 1902.—*Owen, R.*, Fossil Reptiles of the Mesozoic Formations (Mon. Palaeont. Soc.), p. 27, 1875.—*Phillips, J.*, Geology of Oxford, p. 245, 1871.—*Woodward, A. S.*, Skeleton of *Cetiosaurus leedsi.* Proc. Zool. Soc., 1905, vol. i., p. 232.

[2] *Huene, F. von*, Hinterhaupt von *Megalosaurus bucklandi* aus Stonesfield. Neues Jahrb. f. Min., etc., 1906, vol. i., p. 1. Also Eclogae geol. Helvetiae, vol. xx., p. 446, 1927. [Criticised by *Hay, O. P.*, Proc. U.S. Nat. Mus., vol. xxxvi., p. 106, 1909.]

[3] *Hatcher, J. B.*, *Astrodon* (*Pleurocoelus*) in the *Atlantosaurus* Beds of Wyoming. Ann. Carnegie Mus., vol. ii., p. 9, 1903.—*Hulke, J. W.*, Note on *Ornithopsis*, H. G. Seeley (*Eucamerotus*, Hulke). Quart. Journ. Geol. Soc., vol. xxxv., p. 752, 1879; also *loc. cit.*, vol. xxxvi., p. 31, 1880, and vol. xxxviii., p. 372, 1882.—*Janensch, W.*, Wirbeltierfauna der Tendaguruschichten . . . Arten von Sauropoden. Archiv f. Biontologie, vol. iii., p. 82, 1914.—*Longman, H. A.*, *Rhoetosaurus brownei.* Mem. Queensland Mus., vol. ix., p. 1, 1927.—*Lydekker, R.*, Sauropodous Dinosaur from Madagascar. Quart. Journ. Geol. Soc., vol. li., p. 329, 1895.—*Riggs, E. S.*, The *Brachiosauridae.* Field Columbian Mus., Chicago, Publ. 94, Geol. Ser., vol. ii., no. 6, 1904. —*Seeley, H. G.*, Pelvis of *Ornithopsis.* Quart. Journ. Geol. Soc., vol. xlv., p. 391, 1889.—*Thevenin, A.*, Paléontologie de Madagascar: Dinosauriens. Ann. Paléontologie, vol. ii., p. 121, 1907.—*Woodward, A. S.*, *Dinodocus mackesoni.* Geol. Mag. [5], vol. v., p. 204, 1908.

region to sacrum; zygapophyses narrow and close to median line, hyposphene-hypantrum articulation strong. Sacrum of five vertebrae, very broad. Humerus as long as femur. *B. altithorax* Riggs, with humerus 2 m. long. Upper Jurassic (Morrison Formation); western Colorado. *B. brancai* Janensch, with humerus 2·10 m. long. Upper Jurassic and Lower Cretaceous; Tendaguru, Tanganyika Territory, Africa.

Pleurocoelus Marsh. Known only by very small species, with deep narrow teeth (possibly identical with *Astrodon* Johnston). *P. nanus* Marsh, with

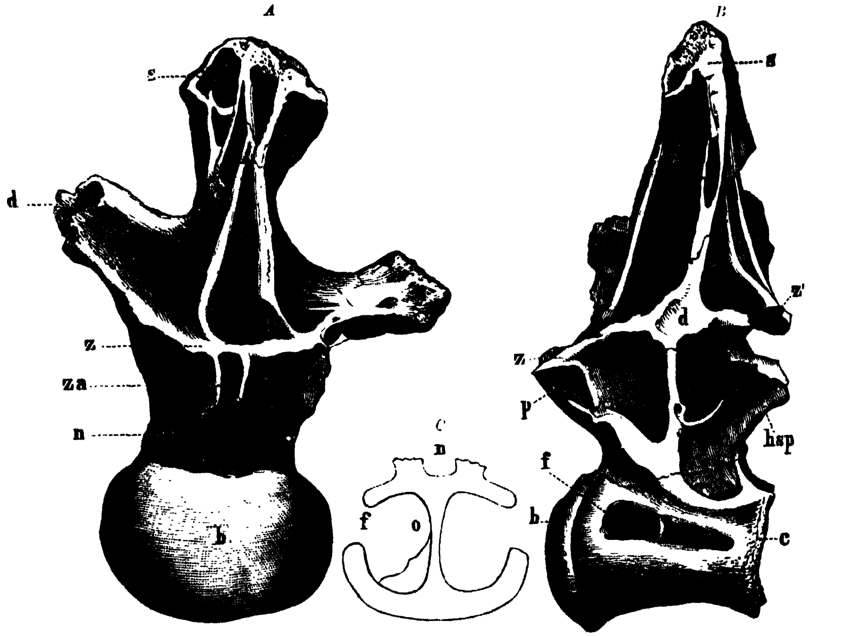


Fig. 485.

Ornithopsis hulkei Seeley. Wealden; Isle of Wight. *A*, Anterior aspect. *B*, Lateral aspect. *C*, Cross-section of dorsal vertebra. *b*, anterior face of centrum; *c*, posterior cup; *d*, transverse process; *f*, lateral air-cavity; *hsp*, hyposphene; *n*, neural canal; *o*, median septum; *p*, capitular facet for rib; *s*, neural spine; *z*, *z'*, pre- and post-zygapophyses; *za*, hypantrum. 1/8 nat. size (after Hulke).

cervical and dorsal vertebrae elongated, not more than 10 cm. in length. Whole skeleton about 4 m. long. Upper Jurassic; Maryland and Wyoming. *P. valdensis* Lydekker. Teeth and vertebra. Wealden; Sussex.

Bothriospondylus Owen. Vertebrae from Lower Jurassic (Forest Marble) and Upper Jurassic (Kimmeridge Clay) of England. *B. madagascariensis* Lydekker, about 15 m. in length, with humerus about 1·30 m. in length. Middle Jurassic; Madagascar.

Ornithopsis Seeley (*Eucamerotus* Hulke; *Chondrosteosaurus* Owen; ? *Pelorosaurus* Mantell; ? *Oplosaurus* Gervais) (Fig. 485). Very light vertebrae, of thin plates of bone; ischium and pubis very broad. *O. hulkei* Seeley, with cervical vertebra about 35 cm., dorsal vertebra about 23 cm. in length. Wealden; Isle of Wight.

Gigantosaurus Seeley (*Ischyrosaurus* Hulke). Fragments from English Kimmeridge Clay.

Dinodocus Owen. Perhaps identical with *Ornithopsis*. Lower Greensand; Hythe, Kent.

Rhoetosaurus Longman. *R. brownei* Longm., represented by vertebrae, femur, and other fragments from the Jurassic of Durham Downs, Queensland, Australia. The average dorsal vertebral centrum measures 18 cm. in length and 24 cm. in width of articular face.

Family 3. Morosauridae.[1]

Snout short, not depressed; narial opening paired and lateral. Dentition powerful. Presacral vertebrae very light, the posterior cervicals and anterior dorsals with the neural spine divided into a symmetrical pair; caudal vertebrae chiefly amphicoelous. Fore leg much shorter than hind leg. Scapula expanded distally. Pubis less widened than in Cetiosauridae; *ischium meeting its fellow distally side to side.* Upper Jurassic and Lower Cretaceous.

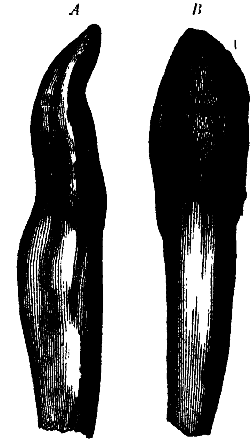


Fig. 486.
Morosaurus grandis Marsh. *A*, *B*, Lateral and anterior aspects of tooth, 1/2 nat. size. Upper Jurassic; Wyoming.

Morosaurus Marsh (Figs. 486, 487). Skull short and deep, with a long close series of teeth. Cervical ribs not fused with their supporting processes. Neck extremely long and flexible, back short, with but ten dorsal vertebrae. Four sacral vertebrae, with cavities in the centra. Lower part of scapula very broad and prominent in front. *M. grandis* Marsh, known by greater part of skeleton about 12 m. long. Upper Jurassic (Morrison Formation); Wyoming. Fragments of the same or a closely allied genus in the Wealden of Sussex.

Camarasaurus Cope. Some associated vertebrae much like those of *Morosaurus*. Upper Jurassic; Colorado.

Amphicoelias Cope. Upper Jurassic; Colorado.

Barosaurus Marsh. Neck unusually large and tail rather short; four sacral vertebrae; the anterior caudal vertebral centra procoelous, with a deep pit on each side. Upper Jurassic; South Dakota.

Gigantosaurus E. Fraas (*nec* Seeley) (*Tornieria* Sternfeld). Sometimes referred in part to *Barosaurus*. Lower Cretaceous; Tendaguru, Tanganyika Territory; also Nyasaland.

The following two genera are allied but may belong to distinct families:

Helopus Wiman. Skull and pelvis much resembling those of *Morosaurus*, but neural spines of cervical and anterior dorsal vertebrae only very slightly

[1] *Fraas, E.*, Ostafrikanische Dinosaurier. Palaeontographica, vol. lv., p. 105, 1908.—*Gilmore, C. W.*, Skeleton of *Camarasaurus*. Mem. Carnegie Mus., vol. x., p. 347, 1925.—*Haughton, S. H.*, *Gigantosaurus dixeyi*. Trans. Roy. Soc. S. Africa, vol. xvi., p. 70, 1928.—*Janensch, W.*, *Dicraeosaurus*. Archiv f. Biontologie, vol. iii., p. 81, 1914.—Das Handskelett von *Gigantosaurus robustus* und *Brachiosaurus brancai*. Centralbl. f. Min., etc., 1922, p. 464.—Material und Formengehalt der Sauropoden in der Ausbeute der Tendaguru-Expedition. Palaeontogr., Suppl. vii., p. 1, 1929.—*Lull, R. S.*, *Barosaurus* Marsh. Mem. Connecticut Acad. Sci., vol. vi., p. 1, 1919.—Skeleton of *Camarasaurus lentus* recently mounted at Yale. Amer. Journ. Sci., vol. xix., p. 1, 1930.—*Osborn, H. F.*, and *Mook, C. C.*, *Camarasaurus*, *Amphicoelias*, and other Sauropods of Cope. Mem. Amer. Mus. Nat. Hist., n.s., vol. iii., p. 247, 1921; also Proc. Amer. Phil. Soc., vol. lviii., p. 386, 1919.—*Wiman, C.*, *Helopus*. Palaeont. Sinica, vol. vi., p. 6, 1929.

forked. Seventeen cervical, fifteen dorso-sacral, three true sacral vertebrae. *H. zdanskyi* Wiman, about 10 m. in length. Lower Cretaceous; Shantung, China.

Dicraeosaurus Janensch. Vertebrae without lateral pits and less cavernous than in *Morosaurus*, with higher neural spines more deeply forked.

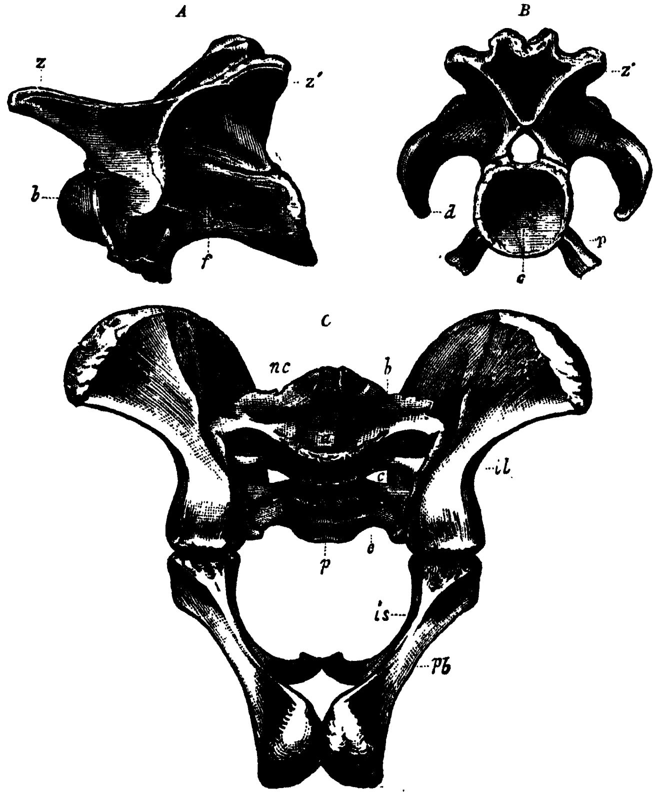


FIG. 487.

Morosaurus grandis Marsh. Upper Jurassic; Wyoming. *A*, *B*, Lateral and posterior aspects of fourth cervical vertebra, 1/8 nat. size. Lettering as in Fig. 485. *C*, Pelvis viewed from in front, 1/16 nat. size. *a-p*, the four sacral vertebrae; *b*, *c*, *e*, transverse processes; *il*, ilium; *is*, ischium; *nc*, neural canal; *pb*, pubis (after Marsh).

Comparatively short neck. Lower Cretaceous; Tendaguru, Tanganyika Territory.

Family 4. **Atlantosauridae.**[1]

Resembling Morosauridae, *but scapula not expanded distally, and ischium meeting its fellow distally end to end.* Upper Jurassic.

Atlantosaurus Marsh. A pituitary canal through the base of the skull. Four sacral vertebrae. *A. montanus* and *A. immanis* Marsh, with femur nearly

[1] *Hatcher, J. B.*, Fore limb and Manus of *Brontosaurus*. Ann. Carnegie Mus., vol. i., p. 356, 1902.—*Holland, W. J.*, *Uintasaurus*. Ann. Carnegie Mus., vol. xv., p. 119, 1924.—*Matthew, W. D.*, The Mounted Skeleton of *Brontosaurus*. Guide Leaflet no. 18, Amer. Mus. Nat. Hist., 1905.—*Riggs, E. S.*, *Apatosaurus* Marsh. Field Columbian Mus., Chicago, Publ. 82, Geol. Ser., vol. ii., no. 4, 1903.

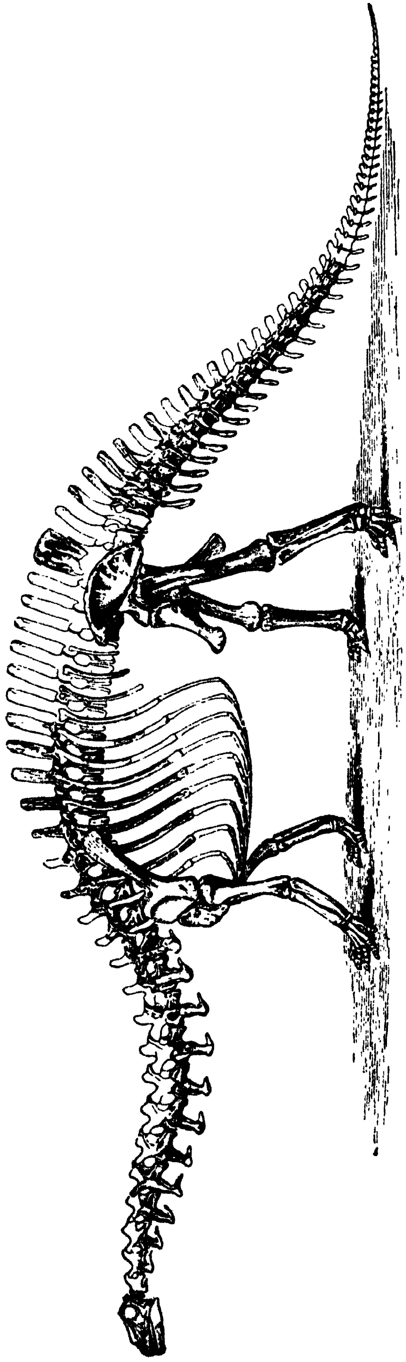


FIG. 488.

Brontosaurus excelsus Marsh. Restoration of skeleton by Marsh, about $1/_{90}$ nat. size. Upper Jurassic; Wyoming. The three lumbar vertebrae should be omitted, and the hypothetical costal cartilages are wrongly drawn.

2 m. long. Upper Jurassic (Morrison Formation); Colorado and Wyoming.

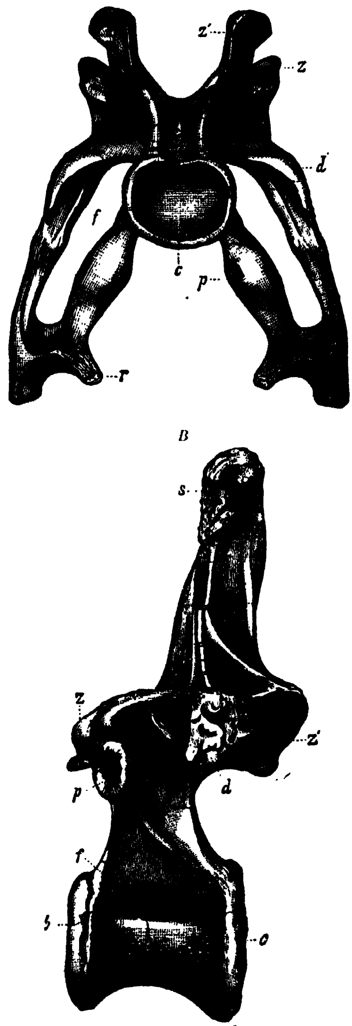


FIG. 489.

Brontosaurus excelsus Marsh. *A*, Posterior aspect of sixth cervical vertebra. *B*, Lateral aspect of dorsal vertebra. Upper Jurassic; Wyoming. Lettering as in Fig. 485. $1/_{12}$ nat. size (after Marsh).

Brontosaurus Marsh (Figs. 488, 489). Skull remarkably small, and brain cavity diminu-

tive. About thirteen cervical vertebrae, with very small neural canal, and no neural spines. Cervical ribs hatchet-shaped, the anterior fused, the hinder articulated with their centra. All the centra deeply hollowed, the inner cavities of the dorsals divided by a narrow median septum. Five sacral vertebrae. Ischia less robust than the pubes, somewhat expanded distally. *B. excelsus* Marsh, known by nearly complete skeleton about 18 m. long. Upper Jurassic; Wyoming. *Apatosaurus ajax* Marsh (type of *Apatosaurus* Marsh) is regarded by Riggs as an immature individual of *Brontosaurus*, with sacral vertebrae incompletely fused.

Uintasaurus Holland. Cervical vertebrae from Upper Jurassic (Morrison Formation), Utah.

Family 5. **Diplodocidae.**[1]

Teeth slender and cylindrical, restricted to front margin of the jaws. External narial opening unpaired, placed at apex of the skull. Presacral vertebrae both hollowed and excavated for lightness. Neural spine of posterior cervical and anterior dorsal vertebrae divided into a symmetrical pair. Caudal vertebrae amphicoelous, except in terminal lash where they have conical ends. Anterior limbs short; scapula much expanded proximally, less expanded distally. Pubis and ischium thickened distally; ischium meeting its fellow distally side to side. Upper Jurassic.

Diplodocus Marsh (Figs. 490, 491). Skull elongated and laterally compressed, elevated behind, depressed at the snout. Orbit very large and high up; a triangular antorbital vacuity and a small maxillary vacuity; supratemporal fossa very small; quadrate much inclined forwards. Neck extremely long and flexible, and back short. Vertebrae much elongated. Fifteen cervicals, ten dorsals, five sacrals, and seventy or more caudals. An unsymmetrical slender curved bone found with the original skeleton of *D. carnegii* has been variously interpreted as clavicle or *os penis*.[2] *D. longus* Marsh and *D. carnegii* Hatcher, about 25 m. long. Upper Jurassic (Morrison Formation); Colorado and Wyoming.

Family 6. **Titanosauridae.**[3]

Much resembling Diplodocidae *but six sacral vertebrae, the first caudal vertebra convex at each end, the following vertebrae procoelous, and pubis not narrowing distally.* Cretaceous.

[1] *Abel, O.*, Die Rekonstruktion des *Diplodocus*. Abh. k. k. Zool.-Botan. Ges. Wien, vol. v., pt. 3, p. 1, 1910.—*Hatcher, J. B.*, *Diplodocus* (Marsh). Mem. Carnegie Mus., vol. i., p. 1, 1901; also *loc. cit.*, vol. ii., p. 72, 1903.—*Holland, W. J.*, Osteology of *Diplodocus* Marsh. Mem. Carnegie Mus., vol. ii., p. 225, 1906; also Amer. Naturalist, vol. xliv., p. 259, 1910.—*Osborn, H. F.*, Skeleton of *Diplodocus*. Mem. Amer. Mus. Nat. Hist., vol. i., p. 191, 1899.

[2] *Nopcsa, F.*, Supposed Clavicle of the Sauropodous Dinosaur *Diplodocus*. Proc. Zool. Soc., 1905, vol. ii., p. 289.

[3] *Broom, R.*, An Opisthocoelian Dinosaur (*Algoasaurus bauri*) in the Cretaceous of South Africa. Geol. Mag. [5], vol. i., p. 445, 1904.—*Depéret, C.*, *Titanosaurus madagascariensis* n. sp. Bull. Soc. Géol. France [3], vol. xxiv., p. 192, 1896.—*Gilmore, C. W.*, New Sauropod Dinosaur from the Ojo Alamo Formation of New Mexico. Smithson. Miscell. Coll., vol. lxxii., no. 14, 1922.—*Huene, F. von*, Rekonstruktion von *Titanosaurus australis*. Eclogae geol. Helvetiae, vol. xx., pl. xvi., 1927.—Die Besonderheit der Titanosaurier. Centralbl. f. Min., etc., 1929, p. 493.—*Lydekker, R.*, Dinosaurs of Patagonia. Anales Mus. La Plata, Paleont. Argentina, vol. ii., p. 1, 1893.—*Nopcsa, F.*, *Titanosaurus dacus*. Quart. Journ. Geol. Soc., vol. lxxix., p. 107, 1923.—*Stromer, E.*, *Aegyptosaurus*. Abhandl. Bay. Akad. Wiss., math.-naturw. Abt., n.f., no. 10, 1932.—*Thevenin, A.*, *Titanosaurus madagascariensis*. Ann. Paléont., vol. ii., p. 133, 1907.

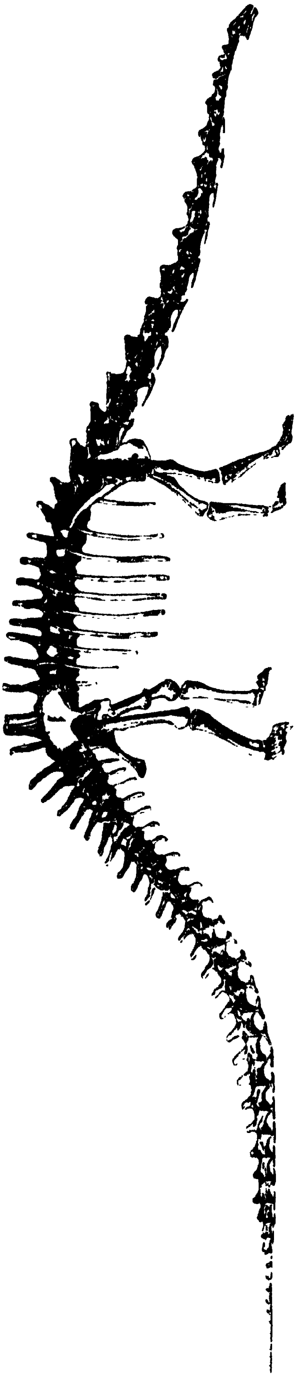


Fig. 490.
Diplodocus carnegii Hatcher. Skeleton. Upper Jurassic; Wyoming. 1/100 nat. size (after Hatcher).

Titanosaurus Lydekker. Scapula with only small forward expansion at base, a little expanded distally; coracoid quadrangular. Small neural arch fixed on anterior half of chief caudal vertebrae; a lash of rod-shaped vertebrae at end of tail. These are characters of *T. australis* Lyd. from the Upper Cretaceous of Patagonia, with femur 70 cm. in length. *T. indicus* Lyd., the type species, founded on a caudal vertebra from Upper Cretaceous (Lameta Beds), India.

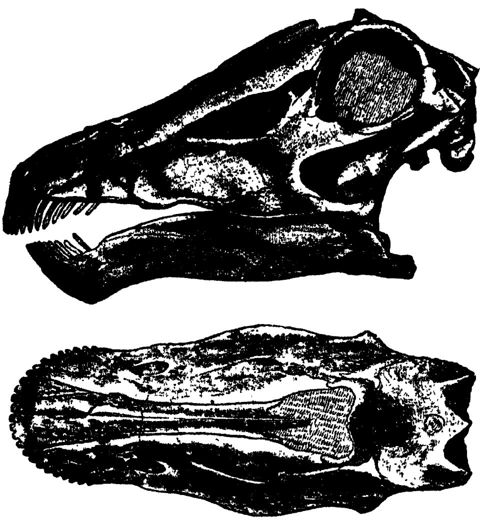


Fig. 491.
Diplodocus longus Marsh. Upper Jurassic; Cañon City, Colorado. Skull and mandible, left lateral and upper aspects. 1/8 nat. size (after Marsh).

Similar vertebrae in Wealden and Upper Greensand, Isle of Wight. Other similar vertebrae and fragments from Brazil, Madagascar, Transylvania, and S. France.

Argyrosaurus Lydekker; *Laplatasaurus*, *Antarctosaurus* F. von Huene; ? *Campylodon* F. von Huene. Patagonia.

Macrurosaurus Seeley. Caudal vertebrae from Cambridge Greensand.

Hypselosaurus Mathéron. Found with spherical egg in Danian (Garumnian) of S. France.

Aepyosaurus Gervais. Aptian; S. France.

Aegyptosaurus Stromer. Cenomanian; Egypt.

Algoasaurus Broom. S. Africa.

Alamosaurus Gilmore. New Mexico.

Teeth of indeterminable Sauropoda have been named *Astrodon* Johnston (Upper Jurassic,

Maryland), *Caulodon* Cope (Upper Jurassic, Colorado), *Morinosaurus* Sauvage (Kimmeridgian, Boulogne), and *Neosodon* de la Moussaye (Portlandian, Boulogne).

B. ORNITHISCHIA.[1]

Reduction of dentition beginning at front end of jaws. Pubis directed forward and downward, not meeting its fellow in the middle line; with a postpubic process inclined backward and downward parallel with the ischium.

Sub-Order 3. ORTHOPODA. (*Predentata* Marsh.)

Herbivorous Dinosaurs, usually large, with completely ossified brain-case, little or no antorbital vacuity in the skull, and toothless predentary bone in front of the mandible. Premaxillae toothless or with small lateral teeth; maxilla and dentary with stout grinding teeth, arranged in one or more functional series. Dentary usually with coronoid process. Teeth usually compressed or spatulate, with serrated anterior and posterior cutting edges, but becoming worn down to flattened stumps with use. External nares large, placed at front end of the skull. Vertebral centra solid, opisthocoelous, amphiplatyan, or sometimes even amphicoelous. Cervical ribs loosely articulated with their centra. Postpubis slender, of variable length; ischium usually with obturator process. Limb bones solid or hollow; anterior extremities shorter than the hinder pair. Astragalus without ascending process; hind feet digitigrade or secondarily plantigrade. No abdominal ribs. Dermal armour sometimes absent, in other cases strongly developed.

This Sub-Order comprises more or less massive herbivorous Dinosaurs, some without armour (*Ornithopoda* Marsh; *Ornithopoidea* Nopcsa), others protected with bony dermal plates (*Stegosauria* and *Ceratopsia* Marsh; *Thyreophoroidea* Nopcsa). The unarmoured forms must have been bipedal in gait, but only the earliest of the armoured forms seem to have been bipedal, their successors with comparatively heavy armour becoming quadrupedal. They are distinguished from the preceding Sub-Orders chiefly by the characters of the pelvis, the presence of a toothless predentary bone, and the usually toothless premaxillae. According to Nopcsa,[2] the males and females among *Orthopoda* can often be distinguished by the characters of the skull, fore arm, and pelvis. In the male the anterior part of the skull is longer, and the posterior part is shorter than in the female, while there are often excrescences; the neural spines of the vertebrae are longer; the fore arm is longer; and the lower end of the ischium is hammer-shaped for the origin of the retractor muscles of the penis. Different specific, or even different generic names may thus have been given to the male and female of the same species.

The earliest *Orthopoda* occur in the Upper Triassic of North America, but they are known only by fragmentary skeletons (*Nanosaurus* Marsh, a very small light-limbed Dinosaur from Colorado, perhaps also *Poposaurus* Mehl, from Wyoming)[3]

[1] *Romer, A. S.*, Pelvic Musculature of Ornithischian Dinosaurs. Acta Zoologica, vol. viii., p. 225, 1927.

[2] *Nopcsa, F.*, Neues über Geschlechtsunterschiede bei Orthopoden. Centralbl. f. Min., etc., 1918, p. 186.—Sexual Differences in Ornithopodous Dinosaurs. Palaeobiologica, vol. ii., p. 187, 1929. See also *Russell, L. S.*, Proc. Amer. Phil. Soc., vol. lxix., p. 159, 1930.

[3] *Broom, R.*, *Geranosaurus*. Ann. S. African Mus., vol. vii., p. 306, 1911.—*Huene, F. von*, and *Lull, R. S.*, Neubeschreibung des Originals von *Nanosaurus agilis* Marsh. Neues Jahrb. f. Min., etc., 1908, vol. i., p. 134.—*Mehl, M. G.*, *Poposaurus gracilis*. Journ. Geol., vol. xxiii., p. 516, 1915.—*Nopcsa, F.*, Zur systematischen Stellung von *Poposaurus* (Mehl). Centralbl. f. Min., etc., 1921, p. 348.

or by footprints (*Anomoeopus* Hitchcock, perhaps also *Eubrontes* Hitch. and *Otozoum* Hitch., from Massachusetts, Connecticut, and New Jersey). A small Orthopod lower jaw (*Geranosaurus* Broom) is also known from the Upper Triassic or Rhaetic Stormberg Beds of Barkly Pass, South Africa. Footprints (*Rigalites* F. von Huene) from the Rhaetic of Ischigualasto, N.W. Argentina, may belong to an armoured Orthopod.[1]

Family 1. **Hypsilophodontidae.**[2]

Probably arboreal. Teeth with enamel reduced on one side; only one row in use. Premaxilla with teeth. Cervical vertebrae more or less opisthocoelous; five sacral vertebrae. Limb bones with large inner cavity. Manus with five digits; III *with four phalanges;* IV *and* V *reduced. Postpubis as long as ischium. Hind foot with four complete digits and rudiment of metatarsal* V. *Dermal armour rudimentary or absent.* Upper Jurassic and Cretaceous.

This and the next family are grouped by Nopcsa as *Kalodontidae.*

Hypsilophodon Huxley. Each premaxilla with five lateral teeth, perhaps toothless in front. Predentary known to be toothless. Enamelled face of tooth with few ridges which end in serrated margin. Ossified tendons across dorsal and caudal neural spines. Pubis not expanded distally. Femur shorter than tibia. Ungual phalanges slender, curved, and pointed. According to Nopcsa without sclerotic plates, but with traces of few bony plates in skin. *H. foxi* Huxley, known by nearly complete skeletons about 1·5 m. long, with skull 10 to 15 cm. long. Wealden; Isle of Wight.

Thescelosaurus Gilmore. Four phalanges definitely known in digit III of manus. Femur longer than tibia. *T. neglectus* Gilm., about 3 m. long. Upper Cretaceous (Laramie or Lance Formation); Wyoming, S. Dakota, Montana, and Saskatchewan. *T. warreni* Parks. Upper Cretaceous (Edmonton Formation); Alberta, Canada.

The following genera seem to belong to this family, but their premaxillae are still unknown:

Laosaurus Marsh. Pubis weak and tapering. Femur about as long as tibia. Upper Jurassic (Morrison Formation); Wyoming and Colorado.

Dryosaurus Marsh. Upper Jurassic; Wyoming and Colorado.

Stenopelix H. von Meyer. Wealden; N. Germany.

Dysalotosaurus Pompeckj. Orbits very large. Nine cervical and sixteen dorsal vertebrae, of which the last is closely united with the four true sacral vertebrae. Femur shorter than tibia. Small first digit of hind foot turned backwards. The type species not much larger than a cat. Kimmeridgian; Tendaguru, Tanganyika Territory.

[1] *Huene, F. von,* Die fossilen Fährten im Rhät von Ischigualasto. Palaeobiologica, vol. iv., p. 99, 1931.

[2] *Gilmore, C. W.,* Osteology of *Thescelosaurus.* Proc. U.S. Nat. Mus., vol. xlix., p. 591, 1915. —*Hulke, J. W.,* Osteology of *Hypsilophodon foxii.* Phil. Trans. Roy. Soc., vol. clxxiii., p. 1035, 1882.—*Koken, E.,* Dinosaurier, etc., norddeutschen Wealden [*Stenopelix*]. Palaeont. Abhandl., vol. iii., p. 309, 1887.—*Nopcsa, F., Hypsilophodon.* Geol. Mag. [5], vol. ii., p. 203, 1905. —*Parks, W. A., Thescelosaurus warreni.* Univ. Toronto Studies, Geol. Ser., no. 21, 1926.— *Pompeckj, J. F., Dysalotosaurus.* Sitzungsb. Ges. naturf. Freunde, Berlin, 1920, p. 120; also Palaeont. Zeitschr., vol. iv., p. 88, 1922.

Family 2. **Iguanodontidae.**[1]

Bipedal, amphibious and terrestrial. Long axis of skull set at right angles to the neck; antorbital vacuity small; premaxilla toothless; mandibular coronoid process strongly developed. Teeth with enamel reduced on one side; only one row in use. Cervical and anterior dorsal vertebrae opisthocoelous; four to six sacral vertebrae. Fore limbs only about half as long as the hinder pair; manus with five digits; III *with three phalanges;* IV *and* V *reduced. Hind foot with three functional digits which are hoofed;* I *reduced or absent;* V *absent. Dermal armour absent.* Upper Jurassic and Cretaceous.

Iguanodon Mantell (Figs. 492-494). Skull (Fig. 493) laterally compressed, with large, nearly terminal nostrils, and small antorbital vacuity. Orbit deeper than wide, smaller than the irregularly triangular or elongated lateral temporal vacuity. Supratemporal vacuities of moderate size, separated by the narrow parietals, which meet in a sharp median crest. Two small supraorbital bones above the eye, but no sclerotic ring. Frontals flattened and apparently fused; nasals elongated. Mandibular suspensorium nearly vertical; articular portion of the quadrate at the base of an unusually deep pedicle. Jugal bounding the orbit and the lateral temporal vacuity inferiorly; quadrato-jugal very small; lachrymal small. Premaxilla with sharp margin originally sheathed with horn. Maxilla and dentary with numerous closely-set teeth in a single row; the teeth (Fig. 494) when unworn are spatulate, loosely socketed, and with serrated margins; successional teeth well formed below those of the

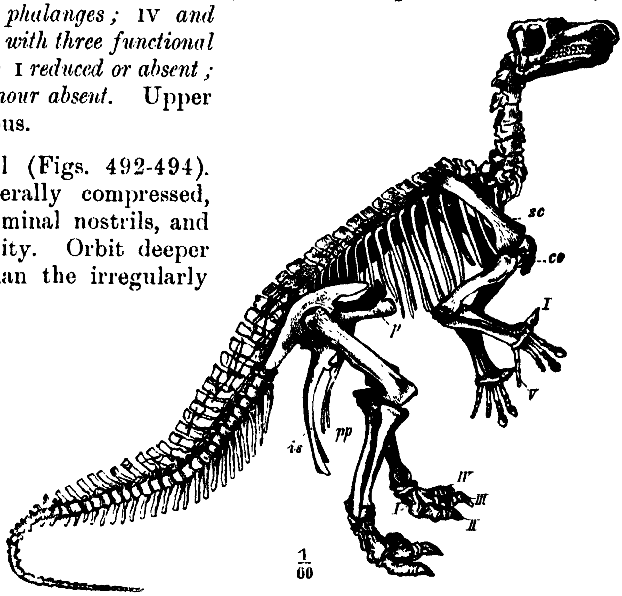


FIG. 492.

Iguanodon bernissartensis Boulenger. Wealden; Bernissart, Belgium. Complete skeleton. *co*, coracoid; *is*, ischium; *p*, pubis; *pp*, postpubic process; *sc*, scapula; *I-V*, digits. 1/60 nat. size (after Dollo).

[1] *Andrews, C. W.*, Brain-cavity of *Iguanodon*. Ann. Mag. Nat. Hist. [6], vol. xix., p. 585, 1897.—*Bertrand, C. E.*, Les Coprolithes de Bernissart. Mém. Mus. Roy. Hist. Nat. Belg., vol. i., p. 1, 1903.—*Dollo, L.*, Dinosauriens de Bernissart. Bull. Mus. Roy. Hist. Nat. Belg., vol. i., pp. 161, 205, 1882; *loc. cit.*, vol. ii., pp. 85, 223, 1883; *loc. cit.*, vol. iii., p. 129, 1884.—*Craspedodon. Loc. cit.*, vol. ii., p. 215, 1883.—Les Allures des Iguanodons. Bull. Sci. France Belg., vol. xl., p. i., 1905.—Le Centenaire des Iguanodons (1822–1922). Phil. Trans. Roy. Soc., vol. ccxii. B, p. 67, 1923.—*Gilmore, C. W.*, Osteology of *Camptosaurus*. Proc. U.S. Nat. Mus., vol. xxxvi., p. 197, 1909; also *loc. cit.*, vol. xli., p. 687, 1912.—*Haughton, S. H.*, Dinosaur Remains from Bushmanland. Trans. Roy. Soc. S. Africa, vol. v., p. 259, 1915.—*Hooley, R. W.*, Skeleton of *Iguanodon atherfieldensis* sp. nov. Quart. Journ. Geol. Soc., vol. lxxxi., p. 1, 1925.—*Nopcsa, F.*, Dinosaurierreste aus Siebenbürgen. Denkschr. k. Akad. Wiss. Wien, math.-naturw. Cl., vol. lxxii., p. 1, 1902; also *loc. cit.*, vol. lxxiv., p. 1, 1904.—Wirbelsäule von *Rhabdodon* und *Orthomerus*. Palaeont. Hungarica, vol. i., p. 273, 1928.—Neues über Geschlechtsunterschiede bei Orthopoden. Centralbl. f. Min., etc., 1918, p. 186.

functional row. Mandibular ramus composed of six pieces, and with slender coronoid process. There are ten cervical, eighteen dorso-lumbar, four to six

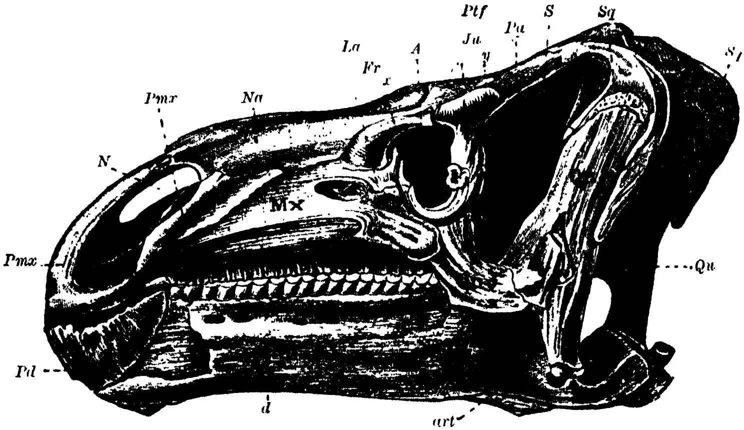


FIG. 493.

Iguanodon bernissartensis Boulenger. Wealden; Bernissart, Belgium. Skull and mandible, left lateral aspect. *A*, orbit; *art*, articular; *d*, dentary; *Fr*, frontal; *Ju*, postfrontal; *La*, lachrymal; *Mx*, maxilla; *N*, external nostril; *Na*, nasal; *Pa*, parietal; *Pd*, predentary; *Pmx*, premaxilla; *Ptf*, postfrontal; *Qu*, quadrate; *QuJ*, portion of jugal, the bone much broken and small quadrato-jugal between it and the quadrate; *S*, lateral temporal vacuity; *Sq*, squamosal; *x*, *y*, supraorbitals (?). 1/8 nat. size (after Dollo).

sacral, and forty to fifty caudal vertebrae. All the presacral vertebrae except the atlas bear ribs, as do also the thirteen anterior caudals. Ossified tendons usually occur along the neural spines of the back and tail. Scapula very long and slender; coracoid small and rounded, notched or perforate at its articular border; a pair of triangular sternal bones. In the hand the pollex is reduced to a single spur-like phalanx; the other digits having a formula of 3, 3, 3, 4. Ilium greatly extended both in front of and behind the acetabulum. Post-pubic process slender and rod-like, shorter than the ischium. Femur scarcely longer than the tibia, and with prominent pendent inner (fourth) trochanter. This, according to Dollo, is distinct from the third trochanter of mammals, and indicates a powerful caudo-femoral musculature, as in birds. Metatarsal I rudimentary, V wanting; the three ungual phalanges broad and hoof-shaped; phalangeal formula of pes, 0, 3, 4, 5, 0. Skin covered with small polygonal epidermal plates, of which some in scattered groups are larger than the others.[1]

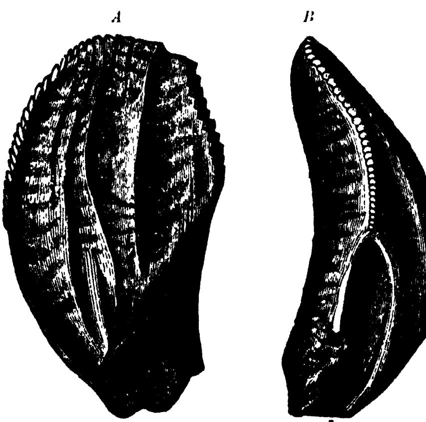


FIG. 494.

Iguanodon mantelli Owen. Wealden; Isle of Wight. Inner (*A*), and posterior (*B*) aspects of mandibular tooth. Nat. size (after Mantell).

[1] *Hooley, R. W.*, Integument of *Iguanodon bernissartensis* and *Morosaurus becklesii*. Geol. Mag. [6], vol. iv., p. 148, 1917.—*Reis, O. M.*, Das Hautskelett von *Iguanodon*. Centralbl. f. Min., etc., 1922, p. 85.

Iguanodon is known by numerous complete skeletons (Fig. 492) from the Wealden of Bernissart, near Mons, Belgium, as many as twenty-three being exhibited in the Brussels Museum. A nearly complete skeleton of *I. atherfieldensis* Hooley is also known from the Wealden of the Isle of Wight. Fragmentary remains occur abundantly in the English Wealden, Lower Greensand, and Purbeckian. The typical species, *I. mantelli* Owen, from the Wealden and Lower Greensand of England, attains a total length of 6 m., and *I. bernissartensis* Boulenger (= *I. seelyi* Hulke) is between 8 and 10 m. long. These are regarded by Nopcsa as probably the male and female of the same species. As proved by its three-toed footmarks (*Struthiopus* Ballerstedt), *Iguanodon* walked on its hind feet in a kangaroo-like attitude, thus leaving the hands free for prehension.

Vectisaurus Hulke; *Sphenospondylus* Seeley. Wealden; Isle of Wight.

Craspedodon Dollo. Tooth from Upper Cretaceous, Lonzée, Belgium. Also *Iguanodon hilli* Newton, from Totternhoe Stone, Hitchin, Herts.

Rhabdodon Mathéron (*Mochlodon* Seeley). Upper Cretaceous; S. France, Austria, and Hungary.

Anoplosaurus Seeley. Cambridge Greensand.

Kangnasaurus Haughton. Cretaceous; Bushmanland, Cape Province, S. Africa.

Cryptodraco Lydekker (*Cryptosaurus* Seeley *nec* Geoffroy). Femur from English Oxford Clay.

Camptosaurus Marsh (*Camptonotus* Marsh *nec* Uhl; ? *Cumnoria* Seeley). The phalangeal formula of the hand is 2, 3, 3, 3, 2, the first three digits bearing pointed claws, the others relatively small and blunt. Postpubis as long as ischium. Femur curved, longer than tibia. Hind foot with four complete digits, but the first comparatively small and short; V represented by the base of the metatarsal. *C. dispar* Marsh, *C. browni* Gilmore, and other species known by skeletons from 6 m. to 10 m. in length, from Upper Jurassic (Morrison Formation), Wyoming. Isolated bones and one imperfect skeleton (*Cumnoria prestwichi* Hulke sp.) from the Oxford and Kimmeridge Clays of England and France, and from the English Wealden, have also been referred to this genus.

Family 3. **Trachodontidae.**[1] (*Hadrosauridae* Cope.)

Bipedal, amphibious and aquatic. As Iguanodontidae, *but teeth more numerous and more than one row in use; snout depressed and laterally expanded; a ring of*

[1] *Abel, O.*, Neue Rekonstruktion von *Trachodon*. Palaeont. Zeitschr., vol. iv., p. 134, 1922.—*Beecher, C. E.*, Reconstruction of *Claosaurus annectens* Marsh. Trans. Connecticut Acad. Sci., vol. xi., p. 311, 1902.—*Brown, B.*, A Crested Dinosaur from the Edmonton Cretaceous [*Saurolophus*]. Bull. Amer. Mus. Nat. Hist., vol. xxxi., art. xiv., 1912; also *loc. cit.*, vol. xxxii., art. xix., 1913.—*Hypacrosaurus*, from the Edmonton Cretaceous of Alberta. *Loc. cit.*, vol. xxxii., art. xx., 1913.—*Corythosaurus casuarius*, a new Crested Dinosaur from the Belly River Cretaceous, with provisional Classification of the Family *Trachodontidae*. *Loc. cit.*, vol. xxxiii., art. xxxv., 1914; also *loc. cit.*, vol. xxxv., art. xxxviii., 1916.—*Prosaurolophus maximus*. *Loc. cit.*, vol. xxxv., art. xxxvii., 1916.—*Gilmore, C. W.*, New Species of *Corythosaurus*, etc. Canadian Field-Naturalist, vol. xxxvii., p. 46, 1923.—New Species of Hadrosaurian Dinosaur from the Edmonton Formation [*Thespesius edmontoni*]. Canada Dept. Mines, Geol. Surv. Bull. no. 38, p. 13, 1924.—Genus *Stephanosaurus*, with a Description of the Type Specimen of *Lambeosaurus lambei* Parks. *Loc. cit.*, p. 29, 1924.—*Hypacrosaurus*. *Loc. cit.*, p. 49, 1924.—*Hatcher, J. B.*, Genera and Species of the *Trachodontidae* (*Hadrosauridae*, *Claosauridae*) Marsh. Ann. Carnegie Mus., vol. i., p. 377, 1902.—*Kräusel, R.*, Die Nahrung von *Trachodon*. Palaeont. Zeitschr., vol. iv., p. 80, 1922.—*Lambe, L. M.*, Manus of *Trachodon*. Ottawa Naturalist, vol. xxvii., p. 21, 1913.—*Grypo-*

sclerotic plates; first digit of manus absent; longer sacrum and powerful hind limbs adapted for swimming. Upper Cretaceous.

Orthomerus Seeley (*Limnosaurus* Nopcsa *nec* Marsh; *Telmatosaurus* Nopcsa; *Hecatosaurus* B. Brown). A primitive Trachodont with comparatively short antorbital region and premaxillae, no antorbital vacuity, and teeth not compressed antero-posteriorly but in the linguo-labial direction. Jugal narrow. Twelve cervical vertebrae, wider than deep, without neural spines. *O. dolloi* Seeley, a femur 50 cm. long and tibia 27 cm. long. Danian; Maastricht, Holland. *O. transylvanicus* Nopcsa, with skull 40 cm. long, known by many parts of skeleton. Danian; Transylvania.

Tanius Wiman. Top of skull flat. Jugal narrow. Humerus little shorter than forearm. *T. sinensis* Wiman, with femur 1 m. long. Upper Cretaceous; Shantung, China.

Syngonosaurus Seeley. Cambridge Greensand.

Mandschurosaurus Riabinin. Related both to *Kritosaurus* and to *Orthomerus*. *M. amurensis* Riab., known by large part of skeleton, with femur 1 m. long. Upper Senonian; Amur River, Siberia.

Kritosaurus B. Brown. Ojo Alamo Formation; New Mexico. Belly River Formation; Alberta, Canada.

Gryposaurus Lambe. Antorbital region of skull comparatively short and upper part of nasal bones raised into a rounded boss. Orbit smaller than lateral temporal vacuity. Belly River Formation; Alberta, Canada.

Edmontosaurus Lambe. Skull high and broad behind, but without crest; orbit much larger than lateral temporal vacuity; premaxilla not extending back so far as orbit; no antorbital vacuity. Sacrum with nine vertebrae. *E. regalis* Lambe, about 10 m. long, with skull over 1 m. long. Edmonton Formation; Red Deer River, Alberta.

Hypacrosaurus B. Brown. Edmonton Formation; Alberta and Montana.

Claosaurus Marsh. Niobrara Formation; Kansas. The so-called *C. annectens* Marsh belongs to *Trachodon*.

Trachodon Leidy (*Hadrosaurus*, *Thespesius* Leidy; *Cionodon*, *Pteropelyx*, *Diclonius* Cope; *Didanodon* Osborn) (Figs. 495-497). Skull elongated, more depressed than in the preceding genera, with large antorbital vacuity, and long and narrow temporal vacuities. No supraorbital crest. Teeth antero-posteriorly compressed, crenulated on the sharp edge, with a median vertical ridge on the enamelled face (Fig. 496); closely arranged in an alveolar groove opening inwardly, with numerous successional teeth (Fig. 497).

saurus notabilis . . . with a Description of the Skull of *Chasmosaurus belli*. *Loc. cit.*, vol. xxvii., p. 145, 1914.—*Cheneosaurus tolmanensis*. *Loc. cit.*, vol. xxx., p. 117, 1917.—Genus *Trachodon* of Leidy. *Loc. cit.*, vol. xxxii., p. 135, 1918.—*Edmontosaurus*. *Loc. cit.*, vol. xxxi., p. 65, 1917.—The Hadrosaur *Edmontosaurus* from the Upper Cretaceous of Alberta. Canada Dept. Mines, Geol. Surv. Mem. 120, 1920.—*Nopcsa, F.*, Dinosaurier aus Siebenbürgen. Denkschr. k. Akad. Wiss. Wien, math.-naturw. Cl., vol. lxviii. p. 1, 1899.—Wirbelsäule von *Rhabdodon* und *Orthomerus*. Palaeontologia Hungarica, vol. i., p. 287, 1928.—*Osborn, H. F.*, Integument of *Trachodon*. Mem. Amer. Mus. Nat. Hist., n.s., vol. i., p. 33, 1912.—*Parks, W. A.*, *Kritosaurus incurvimanus*. Univ. Toronto Studies, Geol. Ser. no. 11, 1921.—*Parasaurolophus walkeri*. *Loc. cit.*, no. 13, 1922.—*Corythosaurus intermedius*. *Loc. cit.*, no. 15, 1923.—*Tetragonosaurus*. *Loc. cit.*, no. 31, 1932.—*Riabinin, A.*, Skeleton of *Trachodon amurense*. Bull. Comité Géol., Leningrad, vol. xliv., p. 1, 1925.—*Mandschurosaurus amurensis* nov. gen. nov. sp., a Hadrosaurian Dinosaur from the Upper Cretaceous of Amur River. Mém. Soc. Paléont. Russie, no. 11, 1930.—*Versluys, J.*, Die Kaubewegungen von *Trachodon*. Palaeont. Zeitschr., vol. iv., p. 80, 1922.—*Wiman, C.*, *Tanius*. Palaeont. Sinica, ser. c, vol. vi., p. 41, 1929.—*Parasaurolophus tubicen* n. sp. aus der Kreide in New Mexico. Nova Acta R. Soc. Sci. Upsala, ser. 4, vol. vii., no. 5, 1931.

About twelve cervical, eighteen dorsal, nine sacral, and sixty caudal vertebrae. Humerus shorter than ulna, which has an olecranon process; phalangeal

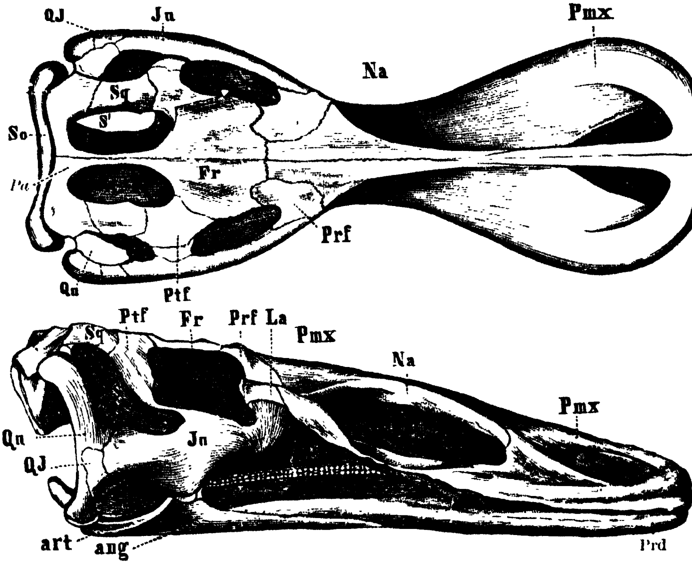


FIG. 495.

Trachodon mirabilis Leidy. Superior and lateral aspects of skull and mandible. Uppermost Cretaceous (Laramie Formation); Dakota. *A*, orbit; *ang*, angular; *art*, articular; *Fr*, frontal; *Ju*, jugal; *La*, lachrymal; *Mx*, maxilla; *N*, antorbital vacuity; *Na*, nasal; *Pa*, parietal; *Pmx*, premaxilla; *Prd*, predentary; *Prf*, prefrontal; *Ptf*, postfrontal; *Qu*, quadrate; *QJ*, quadrato-jugal; *S*, lateral temporal vacuity; *S'*, supratemporal vacuity; *So*, supraoccipital; *Sq*, squamosal. 1/12 nat. size (after Cope).

formula of manus either 3, 3, 3, 3 or 3, 3, 2, 2, the terminal phalange blunt. Postpubis very small and short; ischium not expanded at distal end; femur

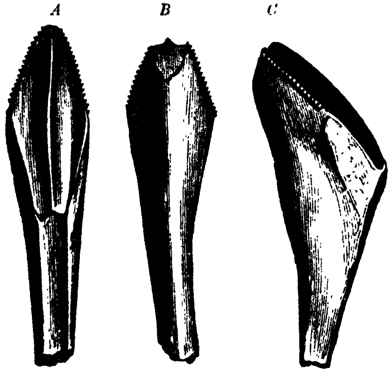


FIG. 496.

Trachodon foulki Leidy sp. Inner (*A*), outer (*B*), and (*C*) lateral aspects of mandibular tooth, somewhat worn. Upper Cretaceous; New Jersey. Nat. size (after Leidy).

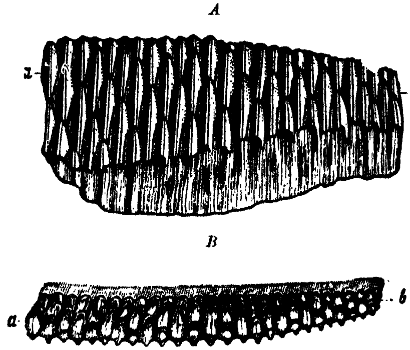


FIG. 497.

Trachodon breviceps Marsh sp. *A*, Inner, and *B*, Superior aspect of functional and successional teeth of dentary. Upper Cretaceous; Montana. 1/4 nat. size (after Marsh).

longer than tibia; no rudiments of digits I, V. Skin covered with rounded or irregularly polygonal epidermal scales, sometimes enlarged and arranged in

rosettes; these epidermal scales also strengthening a segmented median crest on the neck and back. *T. mirabilis* Leidy, the type species founded on teeth from the Judith River, Montana. *T. annectens* Marsh sp., known by a nearly complete skeleton about 9 m. long, and also by a fossilised mummy showing impressions of the skin, from the Laramie Formation of Converse Co., Wyoming. Other species from western North America, New Jersey, North Carolina, and Georgia. *T. cantabrigiensis* Lydekker, a tooth from the Cambridge Greensand.

Saurolophus B. Brown. Skull deep behind, with a horn-like median crest above the eye, formed by the frontals, prefrontals, and nasals. Ischium stout, with a triangular expansion at the distal end. Eight sacral vertebrae. *S. osborni* B. Brown, known by greater part of skeleton about 10 m. long. Edmonton Formation; Red Deer River, Alberta, Canada.

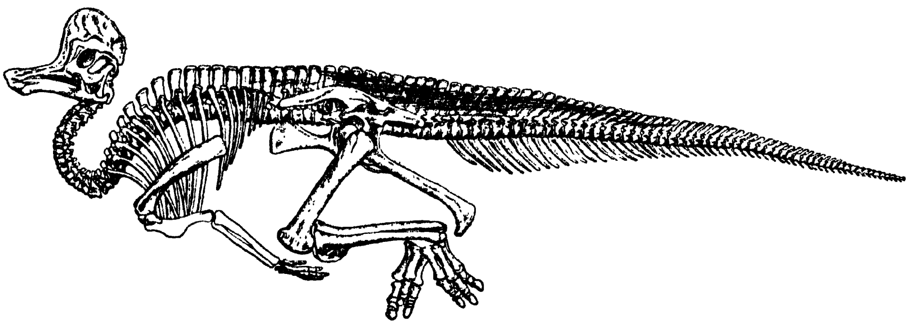


FIG. 498.

Corythosaurus casuarius B. Brown. Skeleton. Upper Cretaceous; Alberta, Canada. 9·35 m. long in matrix (after B. Brown).

Prosaurolophus B. Brown. With incipient supraorbital crest. Distal end of ischium not expanded. Belly River Formation; Alberta.

Parasaurolophus Parks; *Tetragonosaurus* Parks. Belly River Formation; Alberta. *Parasaurolophus* also in New Mexico.

Corythosaurus B. Brown (Fig. 498). A laterally compressed, hollow, rounded crest formed by the backward extension of the premaxillae and nasals above the brain-case; the internal hollow continuous with the nasal cavity, according to Lambe. Narial openings small. Fifteen cervical, nineteen dorsal, and eight sacral vertebrae. Epidermal plates as in *Trachodon*; longitudinal rows of large conical limpet-shaped plates at intervals on the lower surface. *C. casuarius* B. Brown, about 10 m. long. Belly River Formation; Alberta.

Stephanosaurus Lambe (*Lambeosaurus* Parks). Belly River Formation; Alberta.

Cheneosaurus Lambe. Low dome-shaped prominence above and between the eyes. Edmonton Formation; Alberta.

? *Ornithotarsus*, *Pneumatoarthrus*, *Claorhynchus*, *Hypsibema* Cope. *Procheneosaurus* Matthew. North America.

According to Nopcsa, *Parasaurolophus* must be regarded as the male of *Kritosaurus*, *Saurolophus* the male of *Prosaurolophus*, and *Corythosaurus* the male of *Diclonius* (see p. 394). L. S. Russell remarks that the supposed male and female do not always occur on the same horizon.

Family 4. **Psittacosauridae.**[1]

Bipedal. Skull short and deep, broad behind, much laterally compressed at the toothless beak; large orbit with ring of sclerotic plates; no antorbital vacuity; narial openings small, above deepened maxilla. Crown of teeth completely enamelled, compressed to a sharp edge with a blunt apex; few, only one row in use. Neck short, only six cervical vertebrae; five or six sacral vertebrae. Manus reduced by loss of digit V; III *with four phalanges. Pubis and postpubis short and slender; ischium without obturator process. Hind foot with four complete digits and rudiment of metatarsal* V. *Dermal armour doubtful.* Lower Cretaceous.

Psittacosaurus Osborn (Fig. 499). Teeth smooth, not serrated, with a rounded vertical ridge in the middle of the concave face; about nine in the row in

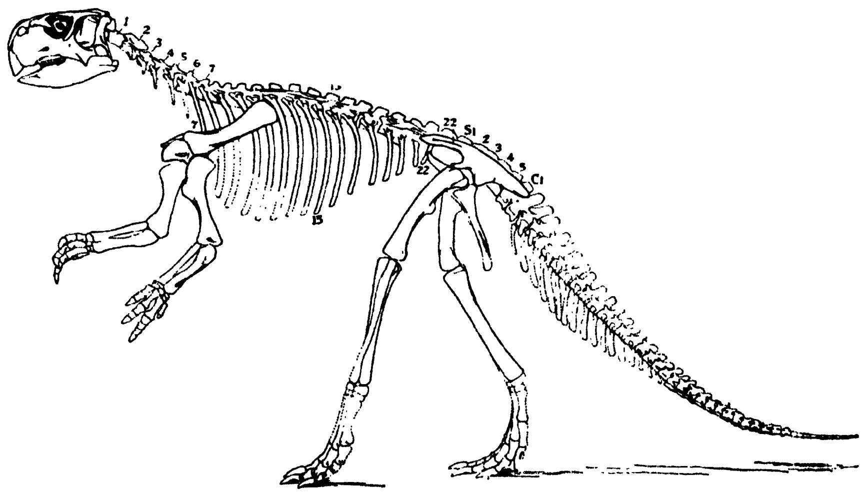


FIG. 499.

Psittacosaurus mongoliensis Osborn. Lower Cretaceous; Mongolia. Much reduced (after Osborn).

both maxilla and dentary. Fifteen or sixteen dorsal vertebrae. Small clavicles identified by Osborn (not yet described). Femur shorter than tibia; hind foot functionally tridactyl, digit I being short. Ungual phalanges pointed. *P. mongoliensis* Osborn, known by greater part of skeleton, about 1·5 m. long. Oshih Formation; Artsa Bogdo, Mongolia.

Protiguanodon Osborn, essentially similar. Ondai Sair Formation; Mongolia.

Family 5. **Stegosauridae.** (*Scelidosauridae* Huxley.)[2]

Skull small and elongated, without antorbital vacuity; narial openings large and far forwards; premaxillae toothless. Teeth small, with a completely enamelled

[1] *Osborn, H. F.*, Two Lower Cretaceous Dinosaurs of Mongolia. Amer. Mus. Novit., no. 95, 1923.—*Psittacosaurus* and *Protiguanodon*. *Loc. cit.*, no. 127, 1924.

[2] *Gilmore, C. W.*, Osteology of the Armored Dinosauria . . . Genus *Stegosaurus*. U.S. Nat. Mus., Bull. 89, 1914; also Proc. U.S. Nat. Mus., vol. xlix., p. 355, 1915, and vol. liv., p. 383, 1918.—*Hennig, E.*, *Kentrurosaurus aethiopicus*. Palaeontographica, Suppl. vii., p. 101, 1925.—*Huene, F. von*, Über den ältesten Rest von *Omosaurus* (*Dacentrurus*). Neues Jahrb. f. Min., etc.,

crown, which is laterally compressed to a sharp crenulated edge, from which proceed vertical striations; one row in use. Vertebrae amphicoelous or amphiplatyan; four or five sacral vertebrae. Fore limbs much smaller than the hinder pair; manus with five short stout digits. Postpubis stout and about as long as the ischium, which lacks an obturator process; hind feet plantigrade, tri- or penta-dactyl, with short, hoof-like, ungual phalanges. Exoskeleton strongly developed, consisting of series of dermal plates and spines. Jurassic.

Stegosaurus Marsh (Figs. 500-502). Skull (Fig. 501) narrow and depressed, relatively very small, and brain cavity in proportion to size of the body more diminutive than in any other land vertebrate. Orbits small, laterally directed, with two supraorbital bones; supratemporal vacuities small and rounded;

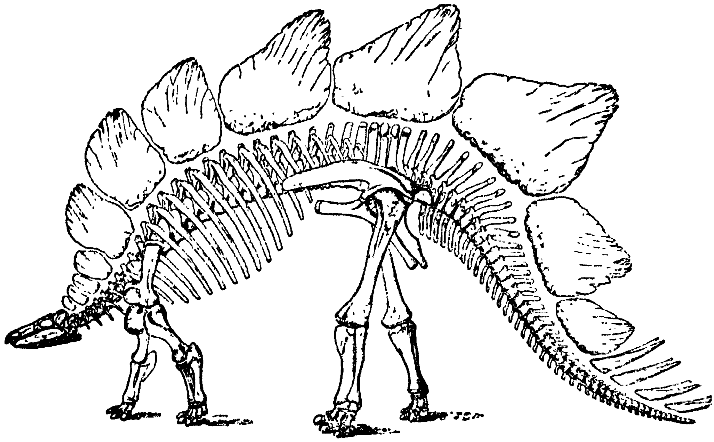


Fig. 500.

Stegosaurus ungulatus Marsh. Restoration of skeleton by Marsh, 1/60 nat. size. Upper Jurassic; Colorado. The dermal plates of the dorsal crest should be shown as a paired series.

nasals nearly half as long as the skull. Mandibular ramus deep, without coronoid process. Teeth over twenty in the row in each maxilla and dentary. Cervical vertebrae with short ribs, and dorsals with much elevated neural arches, on which the stout dorsal ribs are borne. Sacrum of four fused vertebrae, sometimes with one or more lumbars added on in front; their neural canal enlarged to twenty times the capacity of brain cavity (Fig. 502). Anterior caudal vertebrae the largest in the column, and with strong chevron bones. Vertebrae and limb bones solid. Fore limb short and stout, ulna with large olecranon process. Femur large and straight, without inner or fourth trochanter; tibia and fibula much shorter. Astragalus and calcaneum

1910, vol. i., p. 75.—*Hulke, J. W.*, *Omosaurus durobrivensis*. Quart. Journ. Geol. Soc., vol. xliii., p. 699, 1887. [Plates here described belong to the fish *Leedsia*.]—*Janensch, W.*, Ein aufgestelltes Skelett des Stegosauriers *Kentrurosaurus*. Palaeontographica, Suppl. vii., p. 257, 1925.—*Lull, R. S.*, Armor of *Stegosaurus*. Amer. Journ. Sci. [4], vol. xxix., p. 201, 1910.—*Stegosaurus ungulatus* Marsh. *Loc. cit.*, vol. xxx., p. 361, 1910.—*Lydekker, R.*, Jaw of a New Carnivorous Dinosaur [*Sarcolestes*]. Quart. Journ. Geol. Soc., vol. xlix., p. 284, 1893.—*Matley, C. A.*, Armoured Dinosaur from the Lameta Beds. Rec. Geol. Surv. India, vol. lv., p. 105, 1923.—*Nopcsa, F.*, *Stegosaurus priscus*, sp. nov. Geol. Mag. [5], vol. viii., pp. 109, 145, 1911.—*Omosaurus lennieri*. Bull. Soc. Géol. Normandie, vol. xxx., p. 1, 1911.—*Owen, R.*, Reptilia of the Liassic Formation. Mon. Palaeont. Soc., pt. i., p. 1, pt. ii., p. 1, 1861, 1863 [*Scelidosaurus*].—Reptilia of Mesozoic Formations. *Loc. cit.*, pp. 45, 95, 1875.

fused with tibia and fibula; pes tridactyl, digit IV rudimentary, and V want-

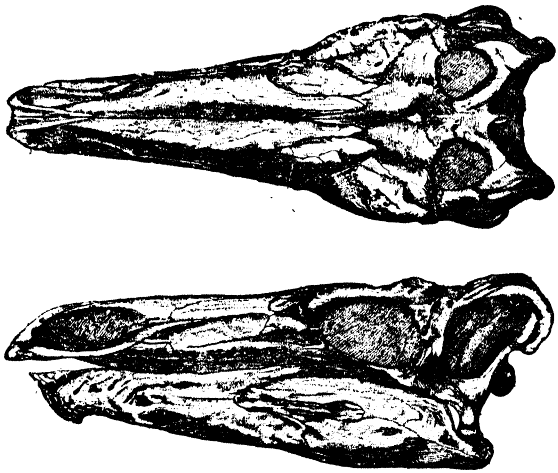


FIG. 501.
Stegosaurus stenops Marsh. Superior and lateral aspects of skull and mandible. Upper Jurassic; Colorado. $^1/_6$ nat. size (after Marsh).

ing. Dermal armour consisting of two rows of erect flattened bony plates extending from the back of the head well down the tail, the largest plates situated immediately over the pelvis. Four spines near end of tail; throat protected by a shield of irregular ossicles. *S. armatus*, *ungulatus* Marsh, and other species, known by nearly complete skeletons 4 to 9 m. long, from the Upper Jurassic (Morrison Beds) of Wyoming and Colorado. *S. priscus* Nopcsa, *S. durobrivensis* Hulke sp. Oxford Clay; Peterborough.

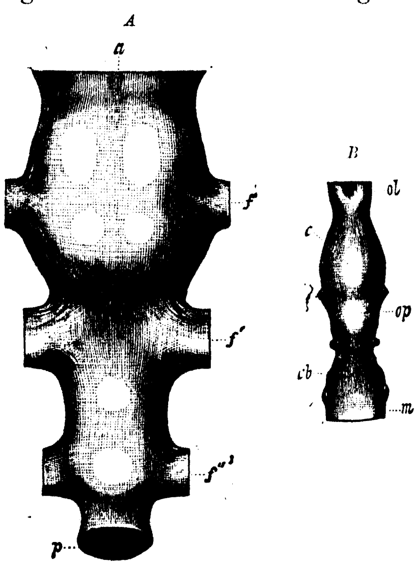


FIG. 502.
Stegosaurus ungulatus Marsh. *A*, Gutta-percha cast of neural canal in sacrum, dorsal aspect, $^1/_4$. *B*, Same of brain cavity. Upper Jurassic; Colorado. *a*, anterior end; *c*, cerebral hemispheres; *cb*, cerebellum; *f*, vacuities between transverse processes of sacrum; *m*, medulla oblongata; *ol*, olfactory lobe; *op*, optic lobe; *p*, posterior end. $^1/_4$ nat. size (after Marsh).

Diracodon Marsh. Probably young of *Stegosaurus*. Upper Jurassic (Morrison Beds); Wyoming.

Scelidosaurus Owen. Dentary with coronoid process. Teeth with triangular or spatulate crowns, coarsely serrated on the margins. All the centra amphicoelous, some with an internal cavity, and the neural canal not expanded. There are six or seven cervicals, sixteen dorsals, one lumbar, four sacrals, and about forty caudals. Femur, tibia, and fibula hollow, the two latter somewhat shorter than the femur and not fused with proximal tarsals. Hind foot functionally tridactyl, the hallux

reduced, and digit V wanting; phalangeal formula 2, 3, 4, 5, 0. Dermal armour of longitudinal series of small tubercles and triangular or conical scutes covering the back and tail. *S. harrisoni* Owen, with skull 25 cm. long, attains a length of 4 m. Lower Lias; England.

Omosaurus Owen (*Dacentrurus* Lucas). Imperfectly known, closely resembling *Stegosaurus*, but ilium not so much elongated anteriorly and rapidly deepening backwards, sacrum with five vertebrae, and neural arches of dorsal vertebrae less elevated. *O. armatus* Owen, with ratio between humerus and femur 4 : 5. Kimmeridge Clay; Wiltshire. *O. lennieri* Nopcsa. Upper Kimmeridgian; Cap de la Hève, Normandy. Femur from Great Oolite, Enslow Bridge, Oxford (*O. vetustus* v. Huene).

Kentrurosaurus Hennig. Much resembling *Stegosaurus*, but neural spines of hinder caudal vertebrae inclined forwards. *K. aethiopicus* Hennig, nearly 5 m. long. Upper Jurassic; Tendaguru, Tanganyika Territory.

Craterosaurus Seeley. Fragment of neural arch of vertebra from Neocomian, Potton, Bedfordshire (F. Nopcsa, Geol. Mag., 1912, p. 481).

Priconodon Marsh. Detached teeth from the supposed Upper Jurassic of Maryland.

Echinodon Owen. Purbeckian; England. Imperfectly known.

?*Sarcolestes* Lydekker. Lower jaw from Oxford Clay, Peterborough.

Family 6. **Acantholidae.**[1] (*Psalisauridae* Lambe.)

Skull small, its long axis at right angles to the rapidly attenuated neck; superior temporal vacuities reduced; quadrate unusually feeble, inclined forwards. No median nuchal plates, but paired bony plates or spines along the back, and flat bony plates on the tail. Cretaceous.

Acanthopholis Huxley. Dentary without coronoid process; lancet-shaped teeth with deep serrations. Cervical vertebrae with flat ends; cross-section of middle and posterior caudals octagonal and hexagonal. Dermal armour of subcircular or oval keeled plates, and of spines which are constricted above the base. *A. horridus* Huxley, probably 3 to 4 m. long. Lower Chalk and Cambridge Greensand; England.

Hylaeosaurus Mantell. Wealden; Sussex and Isle of Wight. The lower jaw named *Regnosaurus* Mantell is referred to this genus by Owen.

Stegoceras Lambe. Skull triangular, ending broadly and squarely behind where the roof overhangs the occiput; parietals and frontals coössified and thickened into a rounded boss, which is marked with pittings. *S. validus* and *brevis* Lambe. Upper Cretaceous (Belly River Formation); Red Deer River, Alberta, Canada. Probably identical with *Troodon* Leidy, founded on teeth from the Judith River Formation, Montana.

Struthiosaurus Bunzel (*Crataeomus*, *Pleuropeltus* Seeley; *Danubiosaurus* Bunzel; *Leipsanosaurus* Nopcsa). Skull less thickened and occiput less

[1] *Gilmore, C. W.*, *Troodon validus*. Univ. Alberta, Dept. Geol. Bull., no. 1, 1924.—New Species of Troodont Dinosaur from the Lance Formation of Wyoming. Proc. U.S. Nat. Mus., vol. lxxix., art. 9, 1931.—*Lambe, L. M.*, *Stegoceras*. Trans. Roy. Soc. Canada [3], vol. xii., sect. iv., p. 23, 1918.—*Nopcsa, F.*, *Leipsanosaurus*. Földtani Közlöny (Budapest), vol. xlviii., p. 324, 1918.—*Acanthopholis*. Geol. Mag., vol. lx., p. 193, 1923.—Dinosaurierreste aus Siebenbürgen. V. Geol. Hungarica, Ser. Palaeont., fasc. 4, 1929 [*Struthiosaurus*, *Rhodanosaurus*].—*Troödon*. Ann. Mag. Nat. Hist., [10], vol. viii., p. 70, 1931 (see also *Russell, L. S.*, *loc. cit.*, vol. ix., p. 334, 1932).

overhanging than in *Stegoceras*. Turonian; Gosau, Lower Austria. Danian; Transylvania.

Rhodanosaurus Nopcsa. Upper Cretaceous; Provence, S. France.

Family 7. **Nodosauridae.**[1] (*Ankylosauridae* B. Brown).

Quadrupedal and armadillo-shaped. Skull relatively larger than in Acanthopholidae *and covered with numerous dermal bony plates; its long axis not at right angles to the short neck. Dentition much reduced. Armour of median nuchal and dorsal bony plates, and numerous paired bony spines or plates.* Cretaceous.

Ankylosaurus B. Brown (*Stereocephalus*, *Euoplocephalus* Lambe). Skull massive and triangular; teeth as in *Stegosaurus*. Vertebrae with flat ends, posterior ribs coössified with vertebrae; neural spines and parapophyses low. All keeled dermal plates low, some fused into a shield. Fore limbs relatively short. *A. magniventris* Brown, known by greater part of skeleton from 4 to 5 m. long, with trunk over 1·5 m. broad. Upper Cretaceous; Montana. Other species in Alberta, Canada.

Palaeoscincus Leidy. Upper Cretaceous; Montana and Wyoming. ? *P. africanus* Broom. Jaw from Lower Cretaceous, Bushman's River, South Africa (*Paranthodon* Nopcsa).

Scolosaurus Nopcsa. Paired triangular dermal spines as well as plates. Tail armour not fused into rings. Humerus twice as long as radius; ratio of humerus to femur 2 : 3. *S. cutleri* Nopcsa, with skeleton about 5 m. long and less than 1 m. high when standing. Upper Cretaceous (Belly River Formation); Red Deer River, Alberta.

Hoplitosaurus Lucas. South Dakota.

Hierosaurus Wieland. Probably as aquatic as turtles. Niobrara Chalk; Kansas.

Nodosaurus Marsh; *Stegopelta* Williston. Benton Cretaceous; Wyoming.

Polacanthus Hulke *ex* Owen. Pelvic region covered with a continuous shield of fused bony plates; paired conical spines on the back and tail. *P. foxi* Hulke, about 3 m. long. Wealden; Isle of Wight.

[1] *Brown, B.*, The *Ankylosauridae*. Bull. Amer. Mus. Nat. Hist., vol. xxiv., p. 187, 1908.—*Gilmore, C. W.*, Skull and Ramus of *Eu[r]oplocephalus tutus* Lambe. Canadian Field-Naturalist, vol. xxxvii., p. 47, 1923.—Dinosaurian Reptiles from the Two Medicine Formation of Montana [skeleton of *Palaeoscincus*, skull of *Dyoplosaurus*]. Proc. U.S. Nat. Mus., vol. lxxvii., art. 16, 1930.—*Hulke, J. W.*, *Polacanthus*. Phil. Trans. Roy. Soc., 1881, p. 653, and 1887, pt. B, p. 169.—*Lambe, L. M.*, *Stereocephalus*. Geol. Surv. Canada. — Contrib. Canadian Palaeont., vol. iii. (4to), p. 55, 1902. — Generic Name *Euoplocephalus*. Ottawa Nat., vol. xxiv., p. 151, 1910.—*Panoplosaurus mirus*. Trans. Roy. Soc. Canada [3], vol. xiii., sect. iv., p. 39, 1920.—*Lucas, F. A.*, New Dinosaur, *Stegosaurus marshi*, from S. Dakota. Proc. U.S. Nat. Mus., vol. xxiii., p. 591, 1901 (=*Hoplitosaurus* Lucas, Science, n.s., vol. xvi., p. 435, 1902).—*Lull, R. S.*, *Nodosaurus textilis* Marsh. Amer. Journ. Sci. [5], vol. i., p. 97, 1921.—*Matthew, W. D.*, Super-Dreadnought of the Animal World. Natural History (Amer. Mus. N. H.), vol. xxii., p. 333, 1922.—*Moodie, R. L.*, Armored Dinosaur [*Stegopelta*] from Wyoming. Kansas Univ. Sci. Bull., vol. v., p. 257, 1911.—*Nopcsa, F.*, *Polacanthus*. Geol. Mag. [5], vol. ii., p. 241, 1905.—*Scolosaurus cutleri*. Geol. Hungarica, Ser. Palaeont., vol. i., p. 54, 1928.—*Parks, W. A.*, *Dyoplosaurus acutosquameus*. Univ. Toronto Studies, Geol. Ser., no. 18, 1924.—*Seeley, H. G.*, Os pubis of *Polacanthus*. Quart. Journ. Geol. Soc., vol. xlviii., p. 81, 1892.—*Sternberg, C. M.*, Supplementary Study of *Panoplosaurus mirus*. Trans. Roy. Soc. Canada [3], vol. xv., sect. iv., p. 93, 1921.—New Armored Dinosaur from the Edmonton Formation of Alberta. *Loc. cit.*, vol. xxii., p. 93, 1928.—Toothless Armoured Dinosaur from the Upper Cretaceous of Alberta. National Museum of Canada, Bull. 54, p. 28, 1929.—*Wieland, G. R.*, *Hierosaurus*. Amer. Journ. Sci. [4], vol. xxvii., p. 250, 1909.—*Williston, S. W.*, *Stegopelta*. Science, n.s., vol. xxii., p. 503, 1905.

Polacanthoides Nopcsa. Limb bones only. Wealden; Sussex.

Panoplosaurus Lambe; *Edmontonia* Sternberg (perhaps identical with *Palaeoscincus*). Alberta.

Anodontosaurus Sternberg. Toothless. Dermal scutes unusually thin. Upper Cretaceous (Edmonton Formation); Alberta.

Dyoplosaurus Parks. Ten vertebrae at end of tail fused and strengthened by ossified tendons, with a ring of bony plates at the tip, forming a club. *D. acutosquameus* Parks, with club 1·3 m. long. Upper Cretaceous (Belly River Formation); Alberta. Upper Cretaceous (Two Medicine Formation); Montana.

? *Metatetrapous* Ballerstedt. Footprints from Wealden, Germany.

? *Lametasaurus* Matley. Upper Cretaceous (Lameta Beds); Jubbulpore, India.

? *Loricosaurus* F. von Huene. Cretaceous; Argentina.

Family 8. **Protoceratopsidae**.[1]

Quadrupedal. Skull large and its long axis continuing that of the neck; parietal bones, and to a lesser extent the squamosal bones, produced beyond the occiput into a crest or frill over the neck; no bony horn-cores on the skull and no dermal bones on the crest. Premaxilla with few teeth, but extremity of beak toothless; teeth in one or two rows, with the roots simple, not bifid. Mandible short and deep. Sacrum of seven or eight vertebrae. Upper border of ilium scarcely inclined outwards; pubis relatively small, but postpubis well developed. Cretaceous.

Protoceratops Granger and Gregory. Skull wide behind, with snout deep and laterally compressed to a beak. Premaxilla with two long, cylindrical teeth. Orbit relatively large. Occipital crest with a pair of transversely oval fontanelles. A loose supraorbital bone. Cervical vertebrae not coalesced; mid-caudal vertebrae with very long neural spines. Fore limb slender, and manus much smaller and shorter than pes. Whole skeleton suggestive of bipedal ancestor. *P. andrewsi* G. and G., with skull 40 to 50 cm. long. Lower Cretaceous; Mongolia. Some skulls relatively longer than others, perhaps male and female.

Leptoceratops B. Brown. Fontanelles in occipital frill smaller. Three anterior cervical vertebrae coalesced. Shorter feet. *L. gracilis* B. Brown, standing about 120 cm. high. Upper Cretaceous (Edmonton Formation); Red Deer River, Alberta, Canada.

Family 9. **Ceratopsidae**.[2]

Quadrupedal. Skull very large and its long axis continuing that of the neck; parietal and squamosal bones produced into a very large crest or frill over the neck;

[1] *Brown, B.*, *Leptoceratops*. Bull. Amer. Mus. Nat. Hist., vol. xxxiii., p. 567, 1914.—*Granger, W.*, and *Gregory, W. K.*, *Protoceratops andrewsi*. Amer. Mus. Novit., no. 72, 1923.—*Gregory, W. K.*, and *Mook, C. C.*, *Protoceratops*. *Loc. cit.*, no. 156, 1925.

[2] *Brown, B.*, *Anchiceratops*. . . . Origin of the Ceratopsian Crest and the Brain Casts of *Anchiceratops* and *Trachodon*. Bull. Amer. Mus. Nat. Hist., vol. xxxiii., p. 539, 1914.—Skull of *Monoclonius*. *Tom. cit.*, p. 567, 1914.—Complete Skeleton of *Monoclonius*. *Loc. cit.*, vol. xxxvii., p. 281, 1917.—*Gilmore, C. W.*, Mounted Skeleton of *Triceratops prorsus*. Proc. U.S. Nat. Mus., vol. xxix., p. 433, 1905.—Skulls of *Triceratops* and *Diceratops*. *Loc. cit.*, vol. xxx., p. 608, 1906.—New Restoration of *Triceratops*, with Notes on the Osteology of the Genus. *Loc. cit.*, vol. lv., p. 97, 1919.—Smallest known Horned Dinosaur, *Brachyceratops*. *Loc. cit.*, vol. lxi.,

a secondary roof with pseudopineal foramen above the frontals; no antorbital vacuity; snout much laterally compressed, with premaxillae coalesced and toothless, and a median rostral bone forming a toothless beak. Teeth in more than one functional row; each tooth with a bifurcated root above the apex of its successor. Bony horn-cores on skull, and usually a row of dermal bones on edge of frill. Neck short, the three anterior vertebrae coalesced. Vertebrae amphiplatyan and solid; about ten sacrals, with no enlargement of neural canal. Paired sternum ossified. Upper border of ilium turned outwards; postpubis much reduced. Upper Cretaceous.

This family is known only from the Upper Cretaceous of Montana, Wyoming, Colorado, New Mexico, and Dakota, U.S.A., and Alberta, Canada. It is chiefly remarkable for the armature of the huge skull, the strong pointed horn-cores of which resemble those of the *Bovidae*. Their rugose outer surface exhibits distinct vascular impressions, and was doubtless sheathed with horn. Internally they are hollow at the base, but become solid higher up.

Ceratops Marsh. Laramie (Lance) Formation; Colorado and Montana.

Eoceratops Lambe. Skull short, deep, and laterally compressed; a pair of slender round horn-cores above the orbits, curving inwards and slightly backwards at the apex; nasal horn-core very short, directed forwards. Occipital crest with a pair of elongated fontanelles in the parietal bones; squamosals broadly triangular; no dermal bones on the margin of the crest. *E. canadensis* Lambe, with skull and crest at least a metre long. Belly River Formation; Red Deer River, Alberta.

Anchiceratops B. Brown. Much resembling *Eoceratops*, but with smaller fontanelles in crest. Edmonton Formation; Alberta.

Arrhinoceratops Parks. Skull short and deep; two large supraorbital horn-cores; crest very large, subquadrate, flat, with pair of small fontanelles. Edmonton Formation; Alberta.

Triceratops Marsh (*Polyonax*, *Agathaumas* Cope) (Figs. 503, 504). Skull more elongated and less deep; a pair of slender round horn-cores above the orbits, very long and directed forwards and usually outwards; nasal horn-core small, directed forwards. Occipital crest without fontanelles; its margin with

art. 3, 1922; also Smithson. Miscell. Coll., vol. lxiii., no. 3, 1914, and U.S. Geol. Surv. Profess. Paper 103, 1917.—Skull of *Eoceratops*. Canadian Field-Naturalist, vol. xxxvii., p. 51, 1923.—*Hatcher, J. B.*, *Lull, R. S.*, and *Osborn, H. F.*, The Ceratopsia. Mon. U.S. Geol. Surv., no. 49, 1907.—*Hay, O. P.*, Skull and Brain of *Triceratops*. Proc. U.S. Nat. Mus., vol. xxxvi., p. 95, 1909.—*Huene, F. von*, Beiträge zur Kenntnis des Ceratopsidenschädels. Neues Jahrb. f. Min., etc., 1911, vol. ii., p. 146, 1912.—*Lambe, L. M.*, Squamoso-parietal Crest of *Centrosaurus* and *Monoclonius*. Trans. Roy. Soc. Canada, ser. ii., vol. x., sect. iv., p. 3, 1904.—Parietal Crest of *Centrosaurus*. Ottawa Naturalist, vol. xxiv., p. 149, 1910.—*Styracosaurus*. *Loc. cit.*, vol. xxvii., p. 109, 1913.—New Genus of *Ceratopsia* [*Protorosaurus*] and the Integument of some Cretaceous Herbivorous Dinosaurs. *Loc. cit.*, vol. xxvii., p. 129, 1914.—*Eoceratops canadensis*, with Remarks on other Genera of Cretaceous Horned Dinosaurs. Geol. Surv. Canada, Museum Bull. no. 12, 1915.—*Lull, R. S.*, Skull of *Triceratops serratus*. Bull. Amer. Mus. Nat. Hist., vol. xix., p. 685, 1903.—Two New *Ceratopsia* [*Diceratops*]. Amer. Journ. Sci. [4], vol. xx., p. 413, 1905.—Cranial Musculature and Origin of Frill in Ceratopsian Dinosaurs. *Loc. cit.*, vol. xxv., p. 387, 1908.—Evolution of the *Ceratopsia*. Proc. 7th Internat. Zool. Congress, p. 771, 1910.—*Parks, W. A.*, *Arrhinoceratops brachyops*. Univ. Toronto Studies, Geol. Ser. no. 19, 1925.—*Sternberg, C. M.*, Integument of *Chasmosaurus belli*. Canadian Field-Naturalist, vol. xxxix., p. 108, 1925.—Homologies of Certain Bones of the Ceratopsian Skull. Trans. Roy. Soc. Canada, ser. iii., vol. xxi., sect. iv., p. 135, 1927.—New Species of Horned Dinosaur from the Upper Cretaceous of Alberta. National Museum of Canada, Bull. 54, p. 34, 1929.—*Wiman, C.*, Ueber Ceratopsia aus der oberen Kreide in New Mexico. Nova Acta R. Soc. Sci. Upsaliensis, ser. 4, vol. vii., no. 2, 1930 [*Pentaceratops*].

a row of small ovoid and conical dermal bones. *T. prorsus* Marsh (Fig. 503), with skull sometimes 2 m. long. Laramie (Lance) Formation; Wyoming. Other species also in Montana and Colorado.

Sterrholophus Marsh (Figs. 505, 506). Perhaps identical with *Triceratops*.

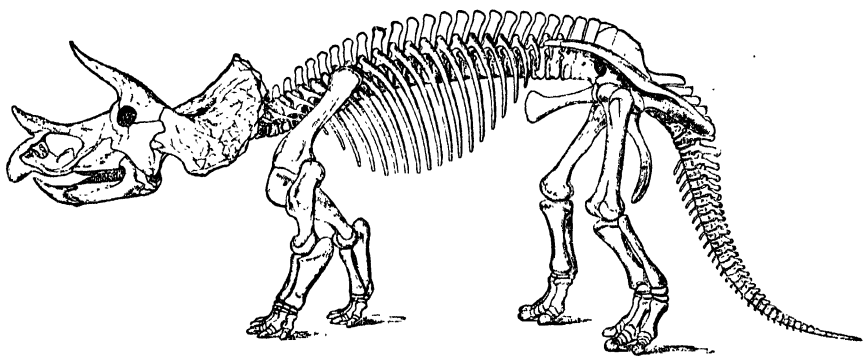


Fig. 503.
Triceratops prorsus Marsh. Restoration of skeleton, $^1/_{70}$ nat. size (after Marsh). Upper Cretaceous; Wyoming.

According to Marsh, a wide margin of the hinder face of the occipital crest in *Triceratops* was free and covered with horn; in *Sterrholophus* the whole of the hinder face of the crest was connected with muscles and ligaments. Laramie (Lance) Formation; Wyoming.

Diceratops Lull (*ex* Hatcher). Skull as in *Triceratops*, but with very small fontanelles in the crest, and without nasal horn-core. Laramie (Lance) Formation; Wyoming.

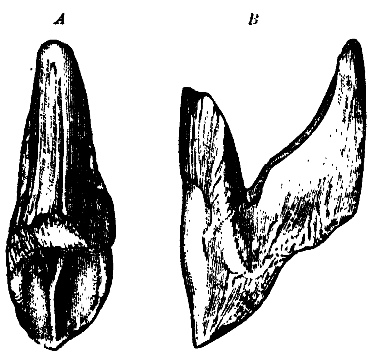


Fig. 504.
Triceratops serratus Marsh. Upper Cretaceous; Wyoming. Outer (*A*) and lateral (*B*) aspect of worn maxillary tooth. Nat. size (after Marsh).

Fig. 505.
Sterrholophus flabellatus Marsh. A vertical series of teeth in succession. Uppermost Cretaceous; Wyoming. *a*, worn apex of tooth in use; *b*, incomplete latest successional tooth. $^1/_2$ nat. size (after Hatcher).

Monoclonius Cope (Fig. 507). Skull short and deep and laterally compressed; supraorbital horn-cores very small, incipient; nasal horn-core long, straight, laterally compressed. A ring of sclerotic plates. Occipital crest

with a pair of large fontanelles in the parietals, a forward and inwardly directed bony process from the hinder margin overhanging each; a row of large dermal bones along the margin. The whole skeleton is known in *M. nasicornus* B. Brown, from the Belly River Formation, Alberta, over 5 m. long. There are twenty-one presacral, ten sacral, and forty-six caudal vertebrae.

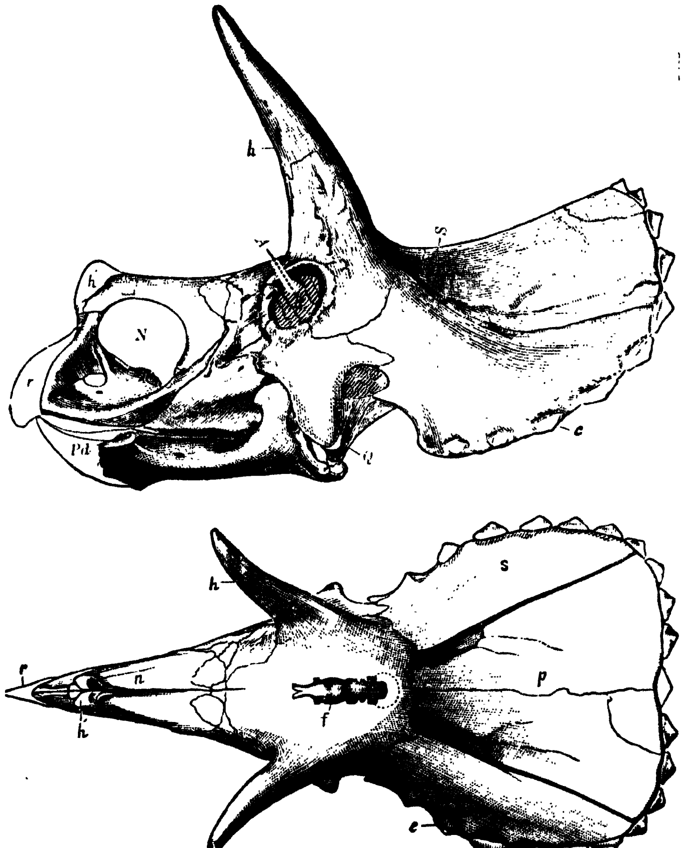


Fig. 506.

Sterrholophus flabellatus Marsh. Lateral and superior aspects of skull. Uppermost Cretaceous; Wyoming. *A*, orbit; *e*, marginal bosses ("epioccipital plates"); *f*, brain; *h*, horn-core; *h'*, nasal horn-core; *N*, external narial opening; *n*, nasal; *p*, parietal; *pd*, predentary (restored in outline); *Q*, quadrate; *r*, rostral bone (restored in outline); *S*, supratemporal vacuity; *s*, squamosal. $^1/_{20}$ nat. size (after Marsh).

The manus has the phalangeal formula 2, 3, 4, 3, 2, and the three inner toes bear hoofs. The hind foot has four functional hoofed toes, with phalangeal formula 2, 3, 4, 5, and the fifth toe is represented by the rudimentary metatarsal. Skin with rounded or polygonal epidermal plates, which do not overlap. Two Medicine Formation; Montana. Belly River Formation; Alberta.

Centrosaurus Lambe. Skull as in *Monoclonius*, but nasal horn-core curved forwards. Belly River Formation; Alberta.

Styracosaurus Lambe. Skull as in *Monoclonius*, but the few dermal bones

on the hinder margin of the parietals in the crest extending backwards as long horns. Belly River Formation; Alberta. Two Medicine Formation; Montana.

Brachyceratops Gilmore. Supraorbital horn-cores very small, nasal horn-core conical and far back. Occipital crest with a pair of small fontanelles and no dermal bones. *B. montanensis* Gilm., with skull about 55 cm. long, and total length of skeleton not much more than 1·5 m. Two Medicine Formation; Montana. *B. dawsoni* Lambe. Belly River Formation; Alberta.

Chasmosaurus Lambe (*Protorosaurus* Lambe *nec* H. v. Meyer). Both supraorbital and nasal horn-cores short and stout; occipital crest with dermal bones on margin, and large fontanelles. Belly River Formation; Alberta.

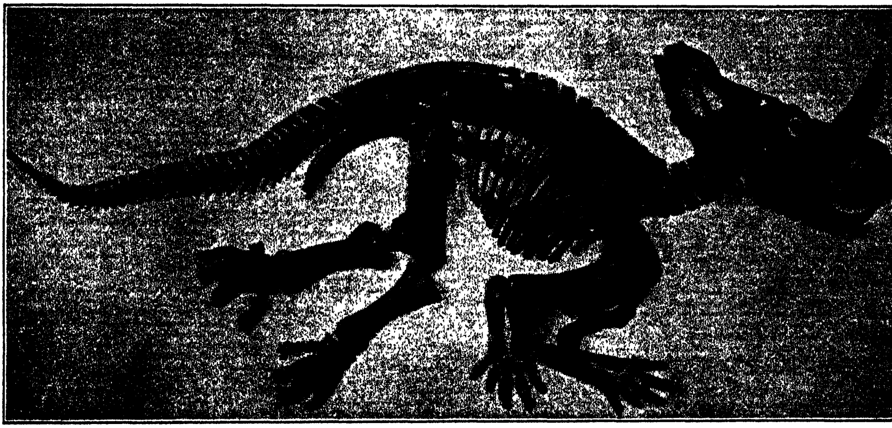


Fig. 507.

Monoclonius nasicornus B. Brown. Skeleton 5·16 m. in length, as found in the rock. Upper Cretaceous; Red Deer River, Alberta, Canada. (After B. Brown).

Torosaurus Marsh. Horn-cores as in *Triceratops.* Occipital crest very large with a pair of fontanelles but no dermal bones. Laramie (Lance) Formation; Wyoming.

Pentaceratops Osborn. Upper Cretaceous (Kirtland Shales); San Juan Co., New Mexico.

? *Notoceratops* F. von Huene. Upper Cretaceous; Patagonia.

Order 14. PTEROSAURIA. (*Ornithosauria* Fitzinger.)[1]

Flying reptiles, with hollow bones, well-formed articulations, and fore limbs adapted for flight. Skull with its long axis extending nearly at right angles to the

[1] *Abel, O.*, Neue Rekonstruktion der Flugsauriergattungen *Pterodactylus* und *Rhamphorhynchus.* Die Naturwissensch., Jahrg. 7, p. 661, 1919.—*Arthaber, G. von*, Entwicklung, Ausbildung und Absterben der Flugsaurier. Palaeont. Zeitschr., vol. iv., p. 1, 1921.—*Branca, W.*, Fossile Flugtiere und Erwerb des Flugvermögens. Abhandl. k. preuss. Akad. Wiss., phys.-math. Kl., 1908, p. 1.—*Döderlein, L.*, Erwerbung des Flugvermögens bei Wirbeltieren. Zool. Jahrb., Abth. f. Systematik, vol. xiv., p. 49, 1901.—Nachtrag zum Carpus und Tarsus der Pterosaurier. Sitzungsb. Bay. Akad. Wiss., math.-naturw. Abt., 1929, p. 175.—*Goldfuss, A.*, Reptilien aus dem lithographischen Schiefer. Nova Acta Acad. Leop., vol. xv., p. 63, 1831.—*Hankin, E. H.*, and *Watson, D. M. S.*, Flight of Pterodactyls. Aeronautical Journ. Gt. Brit., no. 72, 1914.—*Huene, F. von*, Schädel einiger Pterosaurier. Geol. u. Palaeont. Abhandl., n.s., vol. xiii., p. 57, 1914.—*Jaekel, O.*, Flugelbildung der Flugsaurier und Vögel. Anat. Anzeig., vol. xlviii., p. 1, 1915.—*Lambrecht*,

neck. Roofing bones of temporal region contracting into an upper and a lower arch; no pineal foramen; sutures becoming obliterated in the adult. Quadrate large, firmly fixed, inclined downwards and forwards; orbit very large, and usually with sclerotic ring; antorbital vacuity large, sometimes confluent with external nares. Teeth, when present, slender, conical, in sockets, and confined to margin of the jaws. Mandibular rami usually fused at the symphysis. Presacral vertebrae procoelous, caudals amphicoelous; sacrals four to seven in number, usually fused. Cervical and anterior dorsal ribs double-headed. Sternum large, clavicular arch absent, scapula and coracoid long and slender. Fifth digit of manus enormously elongated and reflexed to support the wing-membrane. Pubis and ischium fused; a prepubis. Both rows of tarsals ossified, the astragalus sometimes fused with the tibia. Two to four digits of the pes with claws, the fifth digit sometimes vestigial. Abdominal ribs present; no dermal armour.

The *Pterosauria* or *Ornithosauria* (Pterodactyls) form an extraordinary group of extinct reptiles, ranging from the Lower Jurassic to the Upper Cretaceous. They are remarkably bird-like in general appearance, and their whole organisation is modified for flight, though in most the power of flight was probably more limited than in birds. The skeleton was more or less pneumatic, like that of birds, and the general avian appearance was accentuated by the articulation of the head at right angles to the axis of the neck. Some were no larger than sparrows, but others at the end of the race were of gigantic size, the spread of their wings being nearly 6 m. from tip to tip. Their remains are found chiefly in marine and estuarine deposits, and though many may have fed on insects, some seem to have had a sac below the lower jaw, like the pelicans, and doubtless fed on fishes.

The *vertebral column* comprises seven to nine true cervicals, twelve to sixteen dorsals, four to seven sacrals, and ten to forty caudals. The presacral vertebrae are procoelous, and the caudal amphicoelous. In some of the later Cretaceous genera several of the anterior dorsal vertebrae are fused together and capped by a supraneural plate, to form a *notarium* for strengthening the base of the large wings. The neural arches are usually fused with their centra, and the sides of the latter are more or less extensively hollowed. Cervical ribs, when present, are much shorter than the dorsal ribs. The latter are double-headed anteriorly, but become single-headed and more slender toward the sacral region. Transverse processes are strongly developed in the anterior sacral vertebrae. There is a median series of small abdominal ribs, with one or two lateral pairs.

K., "Elastischen Fasern" des Pterosaurier-Patagiums. Palaeobiologica, vol. ii., p. 57, 1929.—*Meyer, H. von*, Reptilien aus dem lithographischen Schiefer. Fauna der Vorwelt, pt. iv., 1860.—*Newton, E. T.*, Notes on Pterodactyles. Proc. Geol. Assoc., vol. x., p. 406, 1888.—*Nopcsa, F.*, Ideas on the Origin of Flight. Proc. Zool. Soc., 1907, p. 223.—G. von Arthabers Arbeit über Entwicklung und Absterben der Pterosaurier. Palaeont. Zeitschr., vol. vi., p. 80, 1924.—*Plieninger, F.*, Beiträge zur Kenntniss der Flugsaurier. Palaeontogr., vol. xlviii., p. 65, 1901.—Pterosaurier der Juraformation Schwabens. *Loc. cit.*, vol. liii., p. 209, 1907.—*Reck, H.*, Die deutschostafrikanischen Flugsaurier. Centralbl. f. Min., etc., Abt. B, 1931, p. 321.—*Seeley, H. G.*, The Ornithosauria. Cambridge, 1870.—Organisation of the Ornithosauria. Journ. Linn. Soc., Zool., vol. xiii., p. 84, 1876.—The Ornithosaurian pelvis. Ann. Mag. Nat. Hist. [6], vol. vii., p. 237, 1891.—The shoulder-girdle in Cretaceous Ornithosauria. *Loc. cit.*, p. 438, 1891.—Dragons of the Air. London, 1901.—*Wagner, A.*, Contributions on Upper Jurassic Pterosaurs in Abhandl. bayer. Akad. Wiss., math.-phys. Kl., vols. ii., p. 163; vi., pp. 129, 690; viii., p. 439, 1837-58.—*Wiman, C.*, Aus dem Leben der Flugsaurier. Bull. Geol. Inst. Upsala, vol. xix., p. 115, 1924.—Notizen über Flugsaurier. *Loc. cit.*, vol. xxii., p. 217, 1929.—*Zittel, K. A.*, Flugsaurier aus dem lithographischen Schiefer. Palaeontogr., vol. xxix., p. 49, 1882.

The *skull* (Fig. 508) is remarkably bird-like, and its constituent elements usually become anchylosed at an early age. The orbits are very large, laterally placed, and usually surrounded by a sclerotic ring of small plates. An antorbital vacuity is present as in birds and Dinosaurs, and is either confluent with the external nostril on each side, or separated from it by a narrow bar. The supratemporal vacuity is small and placed far backwards. The lateral temporal vacuity appears as a narrow slit behind the orbit, extending downward and forward, and bounded posteriorly by the quadrate. The cranial roof is formed by the large frontals and the smaller parietals, which are without a foramen. At the base of the skull is placed the single occipital condyle, by means of which the head is carried approximately at right angles to the long axis of the neck.

Natural casts of the brain cavity prove it to have been remarkably bird-like, though smaller in proportion to the size of the skull.[1] It was entirely roofed by the frontal, which sometimes extends as far forwards as the anterior border of the orbits, and forms not only their upper, but also a part of their posterior border. The orbit is separated from the lateral temporal vacuity by a trifid postfrontal plate, one branch of which joins the squamosal, and forms at the same time the outer bar of the supratemporal vacuity. The orbit is bounded anteriorly by slender processes of the jugal and prefrontal, which meet each other half-way, both of these plates being small and triangular. The quadrate is a relatively long and narrow bar, united with the squamosal above, and with a buttress of the pterygoid below. In the facial region, which closely resembles that of birds, sutures are always difficult to determine. The snout is pointed in front, or in some cases slightly rounded, and is formed by the enlarged premaxillae, which constitute the greater part of the upper jaw. Teeth, when present, occur in single series at more or less irregular intervals along the margin of the jaws. They are invariably simple and conical, and implanted in distinct sockets. In some genera the sharp margins of the jaws are toothless and may have been sheathed with horn, as in birds.

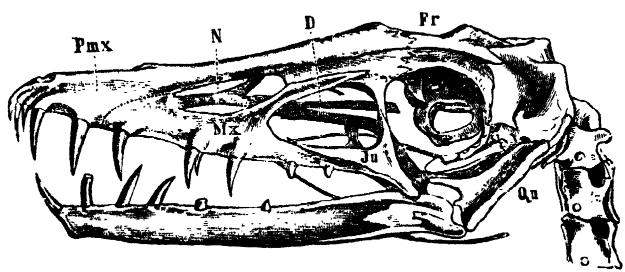


Fig. 508.

Scaphognathus crassirostris Goldf. sp. Skull, mandible, and cervical vertebrae, left lateral aspect. Upper Jurassic; Eichstadt, Bavaria. *D*, antorbital vacuity; *Fr*, frontal; *Ju*, jugal; *Mx*, maxilla; *N*, narial opening; *Pmx*, premaxilla; *Qu*, quadrate. Nearly 2/3 nat. size.

The mandibular rami are straight and elongate, and fused together at the symphysis. They are composed of at least four elements, but the sutures are seldom determinable. A coronoid process is lacking, and the suspensorium is sometimes inclined forwards at a considerable angle, so that the articulation with the quadrate is placed underneath the orbit.

The *pectoral arch* comprises merely a pair of long, narrow scapulae, and

[1] *Edinger, T.*, Das Gehirn der Pterosaurier. Zeitschr. f. Anat. u. Entwick., Abt. Gesammt. Anat., vol. 83, p. 105, 1927.—*Newton, E. T.*, Skull, brain, etc., of *Scaphognathus purdoni*. Phil. Trans. Roy. Soc., vol. 179B, p. 503, 1888.

equally long but somewhat stouter and imperforate coracoids, which articulate with the large sternum by a synovial joint. The sternum is produced in front into a laterally compressed keel to accommodate the enlarged pectoral muscles. There is no clavicular arch, and no precoracoid. The humerus is much

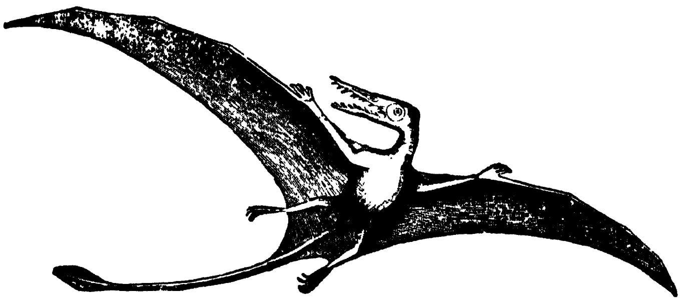


FIG. 509.
Rhamphorhynchus phyllurus Marsh. Restoration, showing extent of cutaneous expansions. Upper Jurassic (Lithographic Stone); Bavaria. $^1/_7$ nat. size (after Marsh).

expanded proximally and exhibits a deltoid crest. The axis of the distal articular facet is approximately at right angles to that of the head of the same bone. The radius and ulna are sometimes twice as long as the humerus, and are about equally developed. The carpal bones are arranged in two rows, and their number varies from three to six.

The metacarpus consists of four bones equal in length, the inner three slender and of nearly similar size, the outermost comparatively stout and

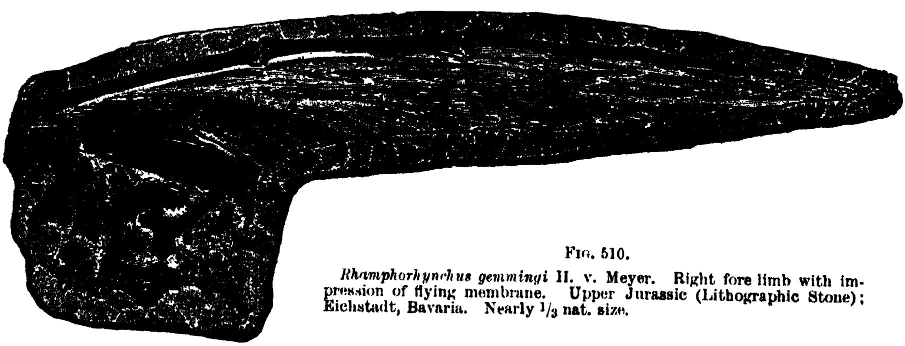


FIG. 510.
Rhamphorhynchus gemmingi H. v. Meyer. Right fore limb with impression of flying membrane. Upper Jurassic (Lithographic Stone); Eichstadt, Bavaria. Nearly $^1/_3$ nat. size.

bearing four elongated phalanges which are turned backward to support the wing-membrane. The three inner metacarpals are sometimes incomplete and taper at their proximal ends to become mere splints on the wing-metacarpal; but they always bear two, three, four phalanges respectively, and the terminal phalange is a large claw. If the small "pteroid bone," which extends backwards towards the shoulder and seems to have strengthened the edge of a strip of membrane, represents the first digit, the wing-finger is the fifth. If it is only an ossified tendon, the wing-finger is the fourth, and the fifth digit is missing.[1] The wing-membrane, or patagium (Fig. 510), is narrow and tapering,

[1] *Plieninger, F.*, Die Hand der Pterosaurier. Centralbl. f. Min., etc., 1906, p. 399.—*Williston, S. W.*, The Fingers of Pterodactyls. Geol. Mag., 1904, p. 59.

in this respect resembling the wing of a swallow or sea-gull. It was attached at its base along the sides of the body wall, and extended beyond the hind limbs to the base of the tail. In at least one genus (*Rhamphorhynchus*) it also formed a leaf-like expansion at the extremity of the tail (Fig. 509). The impressions of the membrane exhibit a number of longitudinal wrinkles or folds, and also numerous fine parallel striae. Broili has described one specimen of *Rhamphorhynchus* which seems to exhibit a covering of fine short hair.[1]

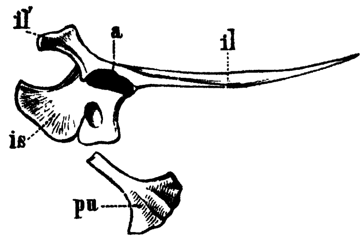


FIG. 511.

Pterodactylus antiquus Sömm. sp. Right lateral aspect of pelvis. Upper Jurassic; Bavaria. *a*, acetabulum, below which is obturator foramen; *il*, ilium; *is*, ischium and pubis; *pu*, prepubis.

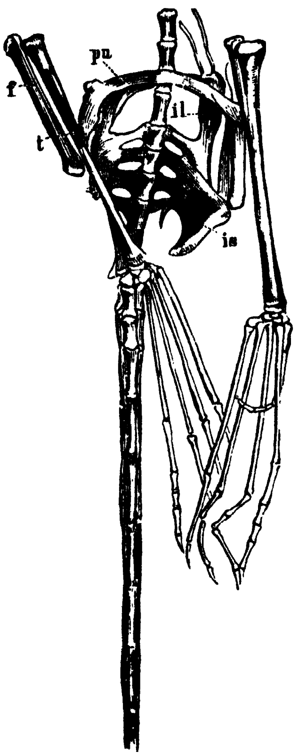


FIG. 512.

Rhamphorhynchus gemmingi v. Meyer. Pelvis, hind limbs, and base of tail. Upper Jurassic; Eichstädt, Bavaria. *f*, femur; *il*, ilium; *is*, ischium; *pu*, prepubis; *t*, tibia. Nat. size.

In the *pelvic arch* (Figs. 511, 512) the ilium is low and extended antero-posteriorly on either side of the imperforate acetabulum as in Dinosaurs, the preacetabular being much longer than the postacetabular portion. Its anterior extremity is sometimes expanded (*Rhamphorhynchus*), in other cases slender and tapering (*Pterodactylus*). The ischium fuses with the pubis, forming a much-expanded bone which is pierced by a small obturator foramen. In front is a prepubis which appears to have been very loosely attached to the antero-inferior portion of the pubis, and almost invariably occurs displaced.[2] In *Pterodactylus* the prepubis is much expanded distally, and was probably united with its fellow in a cartilaginous symphysis; but in *Rhamphorhynchus*, *Pteranodon*, and *Nyctosaurus* it is narrow and band-like, extending forwards for a certain distance, and then bent inwards approximately at a right angle to meet its fellow of the opposite side, with which it may become fused in a ventral symphysis.

The femur is rather longer and more slender than the humerus in some forms, but in others is much shorter, as in birds; and as in birds also, it is exceeded in length by the tibia, which is stout and straight. The fibula is reduced to a mere splint, often fused with the tibia, and its pointed distal end extending scarcely half-way down the shaft of the tibia; or it may be absent altogether. There are two proximal tarsals (astragalus and calcaneum), which in the *Rhamphorhynchidae* and *Ornithocheiridae* are always fused with the tibia. At least two distal tarsals are always present.

[1] *Broili, F.*, Ein *Rhamphorhynchus* mit Spuren von Haarbedeckung. Sitzungsb. Bay. Akad. Wiss., math.-naturw. Abt., 1927, p. 49.

[2] *Huene, F. von*, Praepubisfrage bei Dinosauriern und anderen Reptilien. Anat. Anzeig., vol. xxxiii., p. 401, 1908.

The hind foot is characteristically reptilian in structure. The four inner metatarsals are about equally developed, and bear clawed digits, having the phalangeal formula 2, 3, 4, 5, or sometimes, when the first two digits are clawless, the formula 1, 2, 4, 5. In *Rhamphorhynchus*, at least, these four digits are united by a web for swimming.[1] The fifth digit is almost always shorter than the rest, its metatarsal reduced to a mere stump, sometimes without phalanges, and sometimes with as many as three. In *Rhamphorhynchus* and *Dimorphodon* it was divergent, and doubtless assisted in the support of the patagium. The claws are usually sharp and delicate, and during life were doubtless sheathed with horn.

With one exception, the known Jurassic Pterosaurians are readily divided into a long-tailed Sub-Order, the *Pterodermata* or *Rhamphorhynchoidea*, and a short-tailed Sub-Order, the *Ornithocheiroidea* or *Pterodactyloidea*. The exception is *Anurognathus* Döderlein,[2] represented by a unique imperfect skeleton from the Upper Jurassic (Lithographic Stone) of Eichstädt, Bavaria. It appears to agree in most respects with the first Sub-Order, but has the short tail of the second Sub-Order.

All the known Cretaceous Pterosaurians are *Ornithocheiroidea*.

Sub-Order 1. PTERODERMATA. (*Rhamphorhynchoidea* F. Plieninger.)

Jaws with teeth; external narial opening completely separated from antorbital vacuity. Tail elongated; wing-metacarpal less than half the length of the bones of the fore arm; fifth digit of pes with one to three phalanges.

This group comprises the earlier and more generalised Pterosaurs, all of Jurassic age. Teeth are always present, decreasing in size posteriorly, but sometimes not extending to the anterior end of the jaws. The scapula and coracoid are often fused proximally, and the proximal tarsals are fused with the tibia.

Family 1. Dimorphodontidae.[3]

Antorbital vacuity very large. Prepubis expanded distally. Jurassic.

Dimorphodon Owen (Fig. 513). Skull relatively very large, deepened in form and extremely light; brain case unusually small. External narial openings and antorbital vacuities nearly equal in size. Jaws toothed to the extremity, the anterior teeth very large and irregularly spaced; mandibular suspensorium nearly vertical. Probably four sacral, and at least thirty

[1] *Broili, F.*, *Rhamphorhynchus* mit Resten von Schwimmhaut. Sitzungsb. Bay. Akad. Wiss., math.-naturw. Abt., 1927, p. 29.

[2] *Döderlein, L.*, *Anurognathus ammoni.* Sitzungsb. Bay. Akad. Wiss., math.-phys. Kl., 1923, p. 117; also *loc. cit.*, 1929, p. 47.—*Petronievics, B.*, Über *Anurognathus.* Anat. Anzeig., vol. lxv., p. 214, 1928; also Ann. Géol. Penins. Balkanique, vol. ix., p. 75, 1928.—*Wiman, C.*, Einige Beobachtungen an Flugsauriern. Palaeobiologica, vol. i., p. 363, 1928.

[3] *Arthaber, G.*, Studien über Flugsaurier auf Grund der Bearbeitung des Wiener Exemplares von *Dorygnathus banthensis.* Denkschr. Akad. Wiss. Wien, math.-naturw. Kl., vol. xcvii., p. 1, 1919.—*Newton, E. T.*, *Scaphognathus purdoni.* Phil. Trans. Roy. Soc., vol. 179B, p. 503, 1888.—*Owen, R.*, Reptilia of the Liassic Formations, pt. ii. Mon. Palaeont. Soc., 1870.—*Plieninger, F.*, *Campylognathus zitteli.* Palaeontogr., vol. xli., p. 193, 1895. Also Centralbl. f. Min., etc., 1906, p. 290.—*Salée, A.*, L'Exemplaire de Louvain de *Dorygnathus banthensis.* Mém. Inst. Géol. Univ. Louvain, vol. iv., fasc. iv., 1928.—*Stieler, C.*, Neuer Rekonstruktionsversuch eines liassischen Flugsauriers. Naturwiss. Wochenschr., vol. xxxvii., p. 273, 14th May 1922.—*Wiman, C.*, *Dorygnathus* und andere Flugsaurier. Bull. Geol. Inst. Upsala, vol. xix., p. 23, 1923.

caudal vertebrae, some of the latter with chevron bones. Scapula and coracoid fused. Ischiopubis large, distally expanded. The first four clawed digits of the pes are normal, and the fifth divergent; the latter with a short metatarsal and two phalanges. The skull of *D. macronyx* Owen, the only known species, attains a length of 20 cm. Lower Lias; Dorset.

Dorygnathus Oppel. Skull elongated, and narial opening much smaller than antorbital vacuity. Three or four sacral vertebrae, and a shorter tail than in *Dimorphodon*. *D. banthensis* Theodori sp., with skull about 12 cm. in length. Upper Lias; Bavaria, Würtemberg, and North Germany.

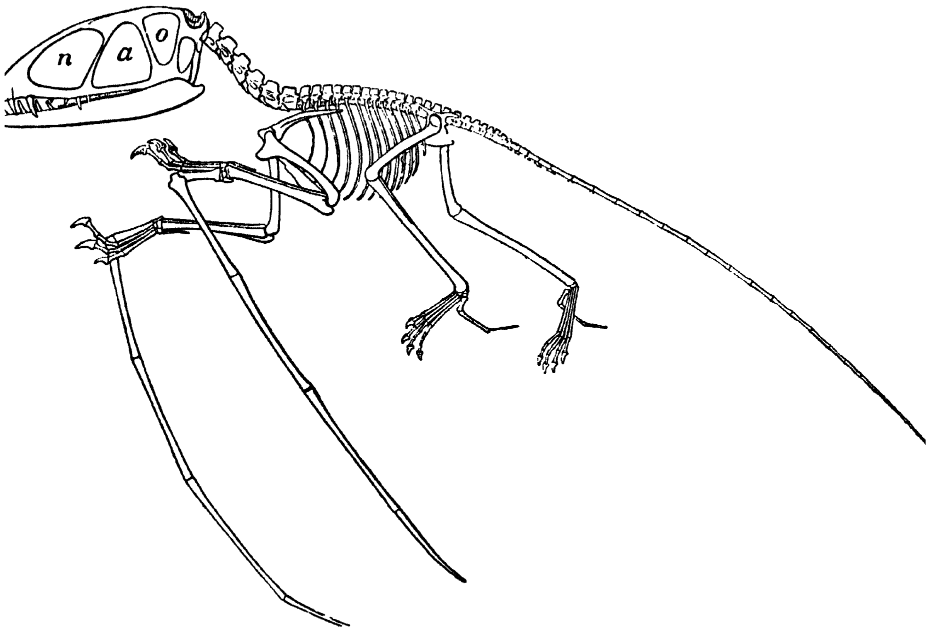


FIG 513.

Dimorphodon macronyx Owen. Restoration of skeleton. Lower Lias; Dorset.
a, antorbital vacuity; *n*, external narial opening; *o*, orbit. 1/7 nat. size (from A. S. Woodward, after Owen).

The following genera may belong either to this family or to the *Rhamphorhynchidae*:

Rhamphocephalus Seeley. Bathonian; Stonesfield, England.

Campylognathus Plieninger. Skull less deep than in *Dimorphodon*, the quadrate more inclined forwards and downwards, and the antorbital and narial openings smaller. Mandibular rami apparently not fused at the symphysis. Four sacral vertebrae. Tail very long. Proximal phalange of wing digit more than double the length of the forearm. Fibula and proximal tarsals fused with tibia. *C. zitteli* Plieninger. Upper Lias; Holzmaden, Würtemberg.

Parapsicephalus Arthaber. Known only by skull, with well-preserved impression of brain. Skull elongated, with gently arched profile and antorbital vacuity larger than orbit; quadrate slightly inclined forwards. *P. purdoni* Newton sp. Upper Lias; Whitby.

Scaphognathus Wagner (Fig. 508). Skull elongated, with depressed

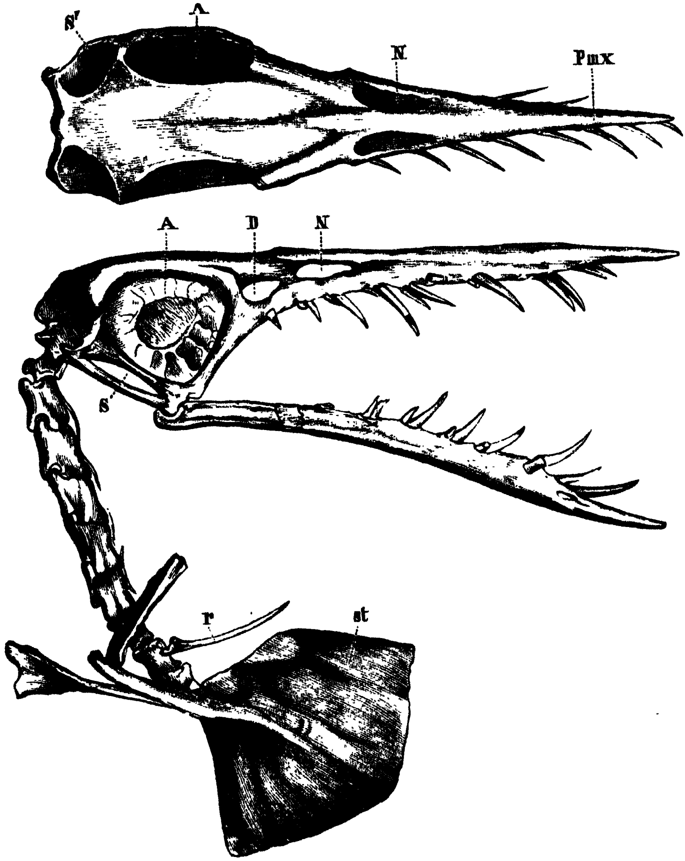


FIG. 514.

Rhamphorhynchus gemmingi H. v. Meyer. Upper Jurassic (Lithographic Stone); Eichstädt, Bavaria. *A*, orbit; *D*, antorbital vacuity; *N*, external narial opening; *Pmx*, premaxilla; *r*, rib; *S*, lateral temporal vacuity; *S'*, supratemporal vacuity; *st*, sternum. About nat. size.

snout and antorbital vacuity smaller than in *Parapsicephalus*. *S. crassirostris* Goldfuss sp., known by imperfect skeleton. Lithographic Stone; Bavaria.

Family 2. Rhamphorhynchidae.[1]

Antorbital vacuity small. Prepubis not expanded distally. Jurassic.

Rhamphorhynchus H. v. Meyer (Figs. 509, 510, 512, 514). Mandibular suspensorium sharply inclined forwards beneath the large orbit. Snout

[1] *Ammon, L. von, Rhamphorhynchus longicaudatus.* Correspondenzbl. Naturw. Ver. Regensburg, Jahrg. 38, p. 129, 1884.—Flughautexemplar von *Rhamphorhynchus*. Geogn. Jahresh. München, vol. xxi., p. 226, 1909.—*Broili, F.*, *Rhamphorhynchus* mit Resten von Schwimmhaut . . . mit Spuren von Haarbedeckung. Sitzungsb. Bay. Akad. Wiss., math.-naturw. Abt., 1927, pp. 29, 49.—*Döderlein, L.*, *Rhamphorhynchus* und sein Schwanzsegel. *Loc. cit.*, 1929, p. 1.—

produced and acuminate; teeth large, irregular, inclined forwards, and not extending to anterior end of the jaws. Orbit very large, with sclerotic ring; narial opening and antorbital vacuity very small. Four sacral and upwards of forty caudal vertebrae. Sternal keel extending downwards as a slender process; scapula and coracoid usually fused. Prepubis in the form of a slender bar, bent inwards nearly at right angles to meet its fellow with which it fuses in a median symphysis. Fifth toe with three phalanges. *R. gemmingi* v. Mey., and larger species with skull sometimes 20 cm. long. Upper Jurassic (Lithographic Stone); Bavaria and Würtemberg. Fragments in Upper Jurassic of Tendaguru, Tanganyika Territory, E. Africa.

? *Doratorhynchus* Seeley. Purbeck Beds.

Sub-Order 2. ORNITHOCHEIROIDEA. (*Pterodactyloidea* F. Plieninger.)

Teeth often reduced, sometimes absent; external narial opening almost or completely united with antorbital vacuity, and this sometimes with orbit. No cervical ribs. Tail short; wing-metacarpal longer or little shorter than forearm; fifth digit of pes vestigial, usually without phalanges.

The members of this Sub-Order vary greatly in size, some being no larger than a sparrow, and the largest having a wing expanse of nearly 6 m. Beginning in the Upper Jurassic, the group culminated in the Upper Cretaceous, and became extinct before the close of that period. It probably includes all known forms of Cretaceous Pterosaurs.

Family 1. Pterodactylidae.[1]

Skull with very small lateral temporal vacuities, and large external narial opening incompletely separated from the antorbital vacuity. Teeth extending to extremity of jaws. Anterior dorsal vertebrae not fused, without supraneural plate. Coracoid and scapula separated, the distal end of the latter spatulate, and not articulating with vertebral column. Elements of carpus and tarsus distinct. Upper Jurassic.

Gilmore, C. W., Skeleton of *Rhamphorhynchus gemmingi.* Proc. U.S. Nat. Mus., vol. xxx., p. 607, 1906.—*Kremmling, W.*, *Rhamphorhynchus gemmingi.* Nova Acta K. Leop.-Carol. Akad. Halle, vol. xcvi., p. 349, 1912.—*Marsh, O. C.*, Wings of Pterodactyles [*Rhamphorhynchus phyllurus*]. Amer. Journ. Sci., vol. xxiii., p. 251, 1882.—*Meyer, H. von*, *Rhamphorhynchus gemmingi.* Palaeontogr., vol. i., p. 1, 1846, and vol. vii., p. 79, 1860.—*Stromer, E.*, Rekonstruktionen des Flugsauriers *Rhamphorhynchus gemmingi.* Neues Jahrb. f. Min., etc., 1913, vol. ii., p. 49. Also Monatsb. Deutsch. Geol. Ges., vol. lxii., p. 85, 1910.—*Wanderer, K.*, *Rhamphorhynchus gemmingi.* Palaeontogr., vol. lv., p. 195, 1908.—*Wiman, C.*, Palaeobiologica, vol. i., p. 365, 1928.—*Woodward, A. S.*, Two Skulls of *Rhamphorhynchus.* Ann. Mag. Nat. Hist. [7], vol. ix., p. i., 1902.

[1] *Abel, O.*, Skeleton of *Pterodactylus antiquus* with remains of Skin and Musculature. Amer. Mus. Novit., no. 192, 1925.—*Broili, F.*, *Pterodactylus micronyx.* Zeitschr. Deutsch. Geol. Ges., vol. lxiv., Abh., p. 492, 1912.—*Pterodactylus* mit Resten der Flughaut. Sitzungsb. Bay. Akad. Wiss., math.-naturw. Abt., 1925, p. 23.—*Ctenochasma gracile* Oppel. Geogn. Jahresh. München, Jahrg. 1916/17, p. 299, 1919.—*Döderlein, L.*, *Pterodactylus* mit Kehlsack und Schwimmhaut. Sitzungsb. Bay. Akad. Wiss., math.-naturw. Abt., 1929, p. 65.—*Fraas, O.*, *Pterodactylus suevicus.* Palaeontogr., vol. xxv., p. 163, 1878.—*Hofker, J.*, *Pterodactylus longirostris.* K. Akad. Wetensch. Amsterdam, vol. xxx., p. 344, 1922.—*Meyer, H. von*, *Pterodactylus spectabilis*, *P. micronyx.* Palaeontogr., vol. x., pp. 1, 47, 1861-62.—*Quenstedt, F. A.*, *Pterodactylus suevicus.* Tübingen, 1855.—*Wiman, C.*, *Pterodactylus westmani* und andere Flugsaurier. Bull. Geol. Inst. Upsala, vol. xx., p. 1, 1925; also Palaeobiologica, vol. i., p. 366, 1928.

Pterodactylus Cuvier (*Ornithocephalus* Sömmering; *Diopecephalus, Cycnorhamphus* Seeley; *Ptenodracon* Lyd.) (Figs. 511, 515, 516). Occiput convex and bird-like. Teeth are small, stout and conical, upright. Four or five sacral vertebrae. All the metacarpals articulate with the carpus. The prepubis is expanded distally. The hind limbs are comparatively large, and the fifth metatarsal bears one phalange. Represented by numerous species

Fig. 515.

Pterodactylus elegans Wagner. Lithographic Stone; Eichstädt, Bavaria. Nat. size.

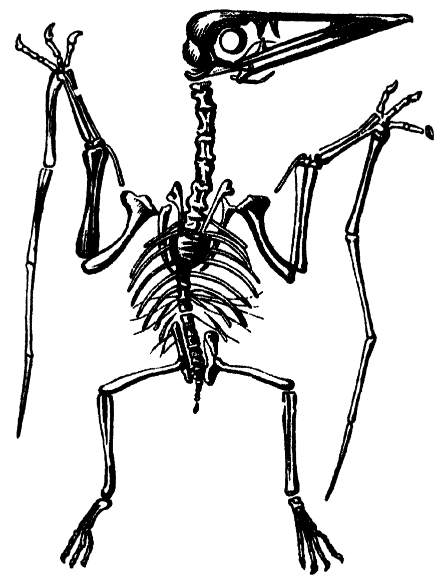


Fig. 516.

Pterodactylus spectabilis H. v. Meyer. Lithographic Stone; Eichstadt, Bavaria. 3/4 nat. size (after H. v. Meyer)

varying in size between that of a sparrow and that of an eagle. The best preserved skeletons occur in the Lithographic Stone of Bavaria, Würtemberg, and Cerin, France. Certain detached fragments from the Kimmeridge and Oxford Clay of England, and from the Upper Jurassic of Tendaguru, Tanganyika Territory, E. Africa, are perhaps referable to this genus.

? *Ctenochasma* H. von Meyer. Teeth extremely numerous, almost bristle-shaped, inclined outwards. Upper Jurassic (Lithographic Stone) and Wealden; Germany.

? *Gnathosaurus* Münster. Lithographic Stone; Bavaria.

Family 2. **Ornithocheiridae.**[1]

External narial opening usually confluent with antorbital vacuity. Teeth, when present, restricted to anterior portion of the jaws. Pectoral arch strong, coracoids

[1] *Eaton, G. F.*, Characters of *Pteranodon*. Amer. Journ. Sci., vol. xvi., p. 82, 1903, and vol. xvii., p. 318, 1904.—Osteology of *Pteranodon*. Mem. Connecticut Acad. Sci., vol. ii., p. 1, 1910. —*Gilmore, C. W.*, New Pterosaurian from Marine Cretaceous of Oregon. Proc. U.S. Nat. Mus.,

and scapulae firmly fused; the former articulating with the sternum, and the latter usually by a large oblique facet with a supraneural plate above the coössified anterior dorsal vertebrae (notarium). Metacarpals of digits II *to* IV *not reaching the carpus but merely splints on the wing-metacarpal. Proximal tarsals fused with the tibia.* Cretaceous.

This family includes the largest known Pterosaurs, their wing expanse varying between 1·5 and 6 m. In these highly specialised forms the anterior extremities attained their greatest power, while the posterior pair were weakened, and probably of slight use as locomotive organs.

Pteranodon Marsh (Fig. 517). Skull considerably elongated, with slender, pointed, toothless jaws, and a long thin supraoccipital crest. Sclerotic ring present. Sternum keelless, but with a stout anterior median projection.

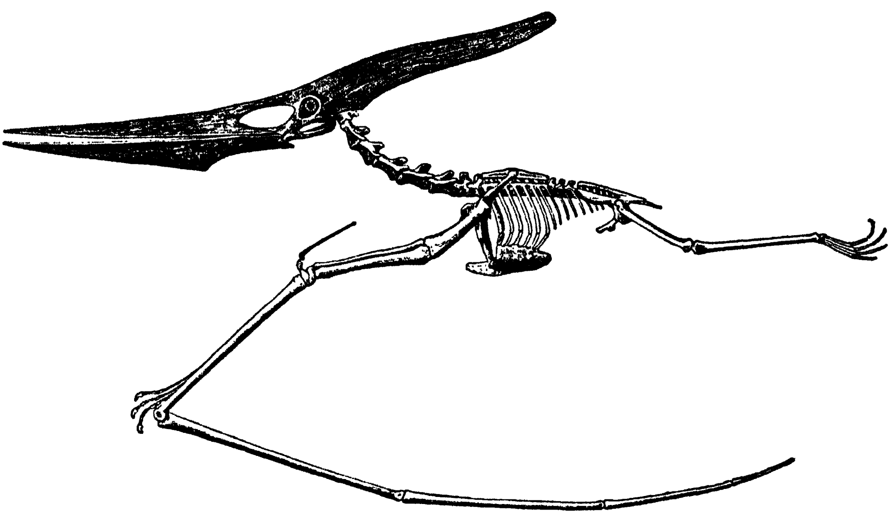


Fig. 517.

Restoration of skeleton of *Pteranodon* by Eaton, much reduced; limbs of the right side omitted. Niobrara Cretaceous; Kansas.

Seven sacral vertebrae. Anterior ribs stout, coössified with their centra. Carpus composed of three bones in two rows. Prepubes band-like, coössified in the middle. Hind limbs relatively small; femur short and curved, with a

vol. 73, art. 24, 1928.—*Hooley, R. W.*, Skeleton of *Ornithodesmus latidens*. Quart. Journ. Geol. Soc., vol. lxix., p. 372, 1913.—*Ornithocheirus*. Ann. Mag. Nat. Hist. [8], vol. xiii., p. 529, 1914.—*Marsh, O. C.*, Skull of *Pteranodon*. Amer. Journ. Sci., vol. xxvii., p. 423, 1884. Earlier notes *loc. cit.*, vol. i., p. 472, 1871; vol. iii., p. 241, 1872; vol. xi., p. 507, 1876; vol. xii., p. 479, 1876; vol. xxi., p. 342, 1881.—*Owen, R.*, Reptilia of Cretaceous Formations, pt. i., 1851, and Suppl. i., 1859. Also Reptilia of Mesozoic Formations, pt. i., 1874. Mon. Palaeontogr. Soc.—*Williston, S. W.*, Kansas Pterodactyls. Kansas Univ. Quarterly, vol. i., p. 12, 1892, and vol. ii., p. 79, 1893.—Restoration of *Ornithostoma* (*Pteranodon*). *Loc. cit.*, vol. vi., p. 35, 1897.—Skeleton of *Nyctodactylus*, with Restoration. Amer. Journ. Anat., vol. i., p. 297, 1902.—Skull of *Nyctodactylus*. Journ. Geol., vol. x., p. 520, 1902.—Osteology of *Nyctosaurus* (*Nyctodactylus*), etc. Field Columbian Mus., Chicago, publ. 78, 1903.—Wing Finger of Pterodactyls, with Restoration of *Nyctosaurus*. Journ. Geol., vol. xix., p. 696, 1911.—*Wiman, C.*, *Pteranodon*. Bull. Geol. Inst. Upsala, vol. xviii., p. 9, 1920.

small trochanter; no separate fibula; tarsus consisting of two free bones in a single row. Fifth digit represented by a small claw-like metatarsal; median phalanges of second, third, and fourth digits very short; first and second digits without claws. *P. occidentalis* Marsh, with span of wing about 6 m., and other species. Niobrara Cretaceous; Kansas. Fragments in marine Cretaceous, Wheeler County, Oregon. Also Russia.

Ornithostoma Seeley, founded on pieces of jaws from the Cambridge Greensand, does not differ generically from *Pteranodon* so far as known.

Nyctosaurus Marsh (*Nyctodactylus* Marsh) (Fig. 518). As *Pteranodon*, but without supraoccipital crest, and the scapula not articulating with the notarium. Seven cervical, twelve dorsal, six sacral, and ten to fourteen caudal

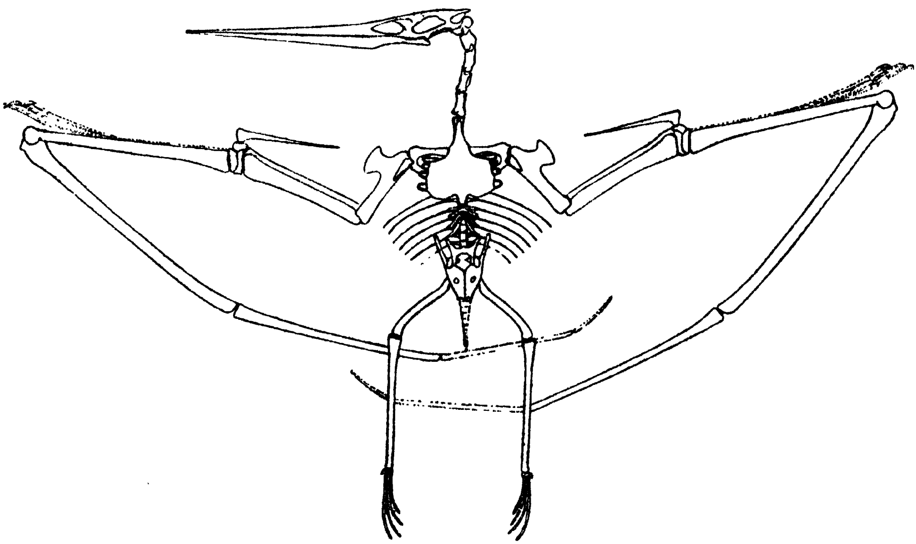


FIG. 518.
Nyctosaurus gracilis Marsh. Niobrara Cretaceous; Kansas. Restoration of skeleton by Williston. 1/9 nat. size.

vertebrae. *N. gracilis* Marsh, with span of wings about 2 m. Niobrara Cretaceous; Kansas.

Ornithocheirus Seeley. Similar in all essential respects to *Pteranodon*, except for the presence of well-developed teeth in both jaws. Front teeth directed forwards. Known only by fragments. Cambridge Greensand; England.

Criorhynchus Owen (*Coloborhynchus* Owen). Snout deep and truncated, teeth inserted vertically. *C. simus* Owen. Cambridge Greensand. Also Wealden species.

Lonchodectes, Amblydectes Hooley. English Cretaceous. *Palaeornis* Mantell. English Wealden.

Dermodactylus Marsh. Upper Jurassic or Lower Cretaceous (Morrison Beds); Wyoming.

Ornithodesmus Seeley. Antorbital vacuity separated by very narrow bar from narial opening. Orbit remarkably small, well behind the quadrate

articulation for the lower jaw. Teeth much laterally compressed, in regular series confined to the end of the snout. No supraoccipital crest. Scapula articulating with the notarium, which consists of six vertebrae. *O. latidens* Seeley, with skull half a metre long. Wealden; Isle of Wight.

Some wing-bones from the Upper Cretaceous of Bohemia, described as *Cretornis hlavatschi* Fritsch, probably belong to one of the foregoing genera. A small Pterosaurian quadrate bone is also known from the Lower Cretaceous of Bahia, Brazil.

Range and Distribution of the Pterosauria.

The earliest undoubted remains of Pterosaurs occur in the Lower Jurassic of Europe, and nothing is known of their ancestors, though *Scleromochlus* (see p. 378) is sometimes regarded as the possible survivor of a group from which they might have originated. The Lower Jurassic genera, which are represented by well-preserved skeletons in the European Lias, are completely adapted for flight, and have a long tail which is still retained by one family in the Upper Jurassic. Small short-tailed forms also appear in the Upper Jurassic, and they agree with their long-tailed contemporaries in having the three clawed wing-digits complete to the base, and the scapula not supported by contact with the backbone. The Jurassic Pterosaurs are scarcely known beyond western Europe. The Cretaceous Pterosaurs are much more widely distributed, and some of the best-preserved skeletons occur in the Chalk of North America. They are all short-tailed, and some are remarkable for their gigantic size, these being the largest known flying animals. In the latest genera of the Order, the metacarpals of the three clawed digits of the hand are reduced to splints which are fixed to the stout wing-metacarpal; and the upper end of the scapula is supported by contact with a mass of fused anterior dorsal vertebrae. The hind limbs are especially weak, and the fibula almost disappears. The jaws are often toothless. When the Pterosaurs included some of the largest forms with the widest geographical distribution, at the end of the Cretaceous period, they rapidly became extinct.

Although Pterosaurs exhibit a number of avian resemblances, they cannot be regarded as the ancestors of birds, and are, in fact, even more widely separated from them than from other Orders of reptiles.

Range and Distribution of Fossil Reptiles.

The earliest known remains of undoubted reptiles occur in Lower **Permian** formations, but they belong to groups which are so varied and so widely spread that they cannot represent the beginning of the Class. Future discoveries in still older formations must reveal more generalised ancestors. Nevertheless, some of the Permian *Cotylosauria* are so closely similar to the Stegocephalian *Temnospondyli*, that they at least may be regarded as reptiles of the most primitive type. They are found most abundantly and in greatest variety in the red beds of the Permian in North America, but they also occur in corresponding rocks in N.W. Russia and in the lower part of the Karroo

Formation in South Africa,[1] besides more sporadically in sandstones near Elgin, Scotland, and in the Rothliegendes of Germany.

Throughout the Permian formations the *Cotylosauria* are associated with a varied series of land reptiles of the Order *Theromorpha*, which seem to include the ancestors of the mammals. In North America the least mammal-like *Pelycosauria* are most abundant, in Europe they are rare. In the Karroo Formation in South Africa the heavy *Dinocephalia* and *Dicynodontia* are very numerous; the former are also found in the Ural, Russia, and the latter in India, N.W. Russia, Scotland, and perhaps in America. In the Karroo Formation the little lizard-shaped *Dromasauria* occur, and the *Therocephalia* represent the first definite approach to the *Mammalia*. There are also the small *Araeoscelidia*, which are best known from North America, but seem to occur in Europe and may perhaps be related to the ancestry of the aquatic *Ichthyosauria* and *Sauropterygia*. The small amphibious or aquatic reptiles of the Order *Mesosauria*, which are found both in Brazil and in South Africa, have actually been regarded as ancestral *Ichthyosauria*. The *Eosuchia* from the Karroo Formation of South Africa are probably forerunners of the *Crocodilia*, and include the aquatic *Tangasauridae* which also occur in Madagascar.

In the **Triassic** the *Cotylosauria* are nearly extinct, being represented only by the specialised family of *Procolophonidae*, which, however, is widely distributed in South Africa, Europe, and North America. The *Theromorpha* now comprise chiefly the *Cynodontia*, which are most numerous in South Africa but are also known from N.W. Russia and Brazil. All the larger species become extinct before the end of the period, but the smaller forms which seem most nearly to approach the mammals linger at least until the Rhaetic. *Ichthyosauria* and *Sauropterygia* retaining many traces of their land-ancestors occur in marine deposits, the former especially in California, Spitzbergen, and south-central Europe, the latter only in Europe and Syria. Most of these Triassic forms are comparatively small. With the ancestral *Sauropterygia* are associated the armoured *Placodontia*. The first *Chelonia* appear in the Upper Keuper of Germany, with most of their distinctive features already well developed. The Diapsidan reptiles now begin to predominate, including early groups of *Rhynchocephalia*, apparent ancestors of the *Crocodilia* and *Dinosauria*, and large species of Saurischian *Dinosauria*. Most of the *Rhynchocephalia* belong to a primitive family, the *Rhynchosauridae*, found in Europe, India, and southern

[1] According to R. Broom and S. H. Haughton, the Karroo Formation of South Africa may be subdivided in descending order as follows:

Stormberg Series	Cave Sandstone	RHAETIC at top
	Red Beds	
	Molteno Beds	
Beaufort Series	Upper Beaufort Beds	TRIASSIC
	Cynognathus Zone	
	Procolophon Zone	
	Middle Beaufort Beds	
	Lystrosaurus Zone	
	Lower Beaufort Beds	PERMIAN
	Cistecephalus Zone	
	Endothiodon Zone	
	Tapinocephalus Zone	
Ecca Series		
Dwyka Series		PERMO-CARBONIFEROUS

Brazil. Closely related to them appear to be the aquatic *Thalattosauridae* from California. The *Thecodontia* probably include the ancestors of both the *Crocodilia* and the *Dinosauria*. Of these the *Pelycosimia* are definitely known only from the Karroo Formation of South Africa, while the *Parasuchia* have never been found there, only in Europe and North America where well-preserved remains are abundant. The Thecodont *Pseudosuchia* are more widely spread in South Africa, Europe, and North America, and one of the latest genera (*Sphenosuchus*) is almost a typical Crocodilian. Nearly all the Triassic *Dinosauria* are carnivorous Saurischians of the Sub-Order *Theropoda*, and some of them seem to be related to the ancestors of the *Sauropoda*. Many of them are comparatively small, but some are unexpectedly large, and their distribution is very wide—Europe, India, South Africa, Australia, and North America. Of Ornithischian *Dinosauria* only a few unsatisfactory specimens have been found in North America and South Africa. Many Triassic *Dinosauria* are known only by footprints, especially in North America.

In the **Jurassic** there are no longer *Theromorpha* and *Thecodontia*. The other Orders are represented by more advanced and more numerous families, and the *Crocodilia* and *Pterosauria* first appear. Typical *Ichthyosauria* and *Plesiosauria* are abundant, ranging from the Lower Lias upwards in Europe, with a few specialised forms in the later Jurassic rocks of North America. Some Upper Liassic *Ichthyosauria* and the Oxfordian and Kimmeridgian *Pliosauridae* attain a gigantic size. The Lower Jurassic *Chelonia* remain still unknown, but there are several Upper Jurassic genera in Europe, a few in North America, all belonging either to the primitive *Amphichelydia* or to the *Pleurodira*. The Upper Jurassic *Rhynchocephalia* are closely similar to the existing *Sphenodon*, though some may have been more aquatic. The *Squamata* are very doubtfully represented. The *Crocodilia*, which range from the Upper Lias upwards in Europe, belong to the Mesosuchian grade and are nearly all marine. One genus (*Steneosaurus*) is also known from the Middle Jurassic of Madagascar, and the marsh-dwelling *Goniopholis* appears first in the Purbeck Beds of England and the Upper Jurassic of North America. The *Metriorhynchidae* are crocodiles adapted for life in the open ocean, and occur in the Middle and Upper Jurassic not only of Europe but also of Patagonia, South America. The *Dinosauria* are widely distributed and attain their greatest development at the end of the Jurassic period. The *Theropoda* range from the Lower Lias upwards in Europe, and are represented by fine skeletons in the Upper Jurassic of North America. They are known to have lived also in Australia. The *Sauropoda* include gigantic species in the Middle and Upper Jurassic of Europe, the Upper Jurassic of Tanganyika Territory, Africa, and North America, and the Jurassic of Madagascar and Queensland, Australia. The armoured *Orthopoda* begin with *Scelidosaurus* in the Lower Lias of southern England, but are especially characteristic of the Middle and Upper Jurassic in Europe and North America, and also occur in the Upper Jurassic of Tanganyika Territory, Africa. The Iguanodont *Orthopoda* also appear in the English Oxford Clay, are well known in the Upper Jurassic of North America and Tanganyika Territory, Africa, and seem to be represented by *Iguanodon* itself in the English Purbeck Beds. The oldest known *Pterosauria* occur as good skeletons in the Lower Lias of Lyme Regis, England, and remains of other genera are well preserved in the Upper Lias of Würtemberg and Bavaria. These are all long-tailed forms, and so also is the Upper Jurassic *Rhamphorhynchus*; but with the

latter is associated the earliest short-tailed Pterodactyl, *Pterodactylus* itself, which is represented by comparatively small species. Jurassic Pterodactyls are scarcely known outside Europe, but a few fragments have been found in the Tendaguru beds in Tanganyika Territory, Africa.

Through the estuarine Wealden Formation of western Europe and equivalent deposits in North America, Tanganyika Territory, and China, the Jurassic reptiles pass gradually into those of the **Lower Cretaceous** period. The division between the Upper Jurassic and Lower Cretaceous estuarine and fluviatile deposits is, indeed, difficult to determine. The *Ichthyosauria* and *Plesiosauria* have now a wider geographical distribution. The *Chelonia* are still chiefly *Amphichelydia* and *Pleurodira*, but Cryptodiran marine turtles begin to occur in China and Australia. Undoubted *Squamata* are found for the first time, both the marine *Dolichosauridae* and primitive *Ophidia* being represented by complete skeletons in the Neocomian of S.E. Europe. The marsh *Crocodilia* of the family *Goniopholidae* are specially characteristic of the European Wealden, and have been found in a similar formation in Bahia, Brazil. Marine crocodiles of the family *Metriorhynchidae* range upwards into the Neocomian of France and Germany. Small Eusuchian *Crocodilia* with procoelous vertebrae also begin to appear in the Wealden. The *Dinosauria* are essentially similar to those of the Upper Jurassic, and include gigantic *Sauropoda* in Europe, Tanganyika Territory, Brazil, and Argentina. The curious Orthopodous *Psittacosauridae* occur in Mongolia, and *Iguanodon* is specially characteristic of the European Wealden. Among *Pterosauria*, the highly specialised *Ornithocheiridae* are represented by *Ornithodesmus* in the English Wealden.

The **Upper Cretaceous** land reptiles are best known from North America, but good examples of the marine groups are more widely spread. The *Ichthyosauria* are fewer than in the Jurassic, but they range from Europe to India, Ceram, Australia, New Zealand, and North and South America. Among *Plesiosauria* the long-necked *Elasmosauridae* are almost as widely distributed. Marine Cryptodiran *Chelonia* now abound, and are particularly well known from North America. They include apparently the ancestors of the *Dermochelyidae*. Among other *Chelonia* the earliest *Trionychoidea* are especially interesting in the fluviatile and land deposits in North America. The *Rhynchocephalia* are represented by the marine *Champsosauridae* both in Europe and North America; and large marine *Squamata*, known as Mosasaurs or *Pythonomorpha*, range from Europe to Palestine, Nigeria, South Africa, North and South America, and New Zealand. They are the characteristic marine reptiles of the period. Among *Crocodilia* there are still Mesosuchians, which include the short-snouted *Notosuchidae* in Patagonia and Egypt; but the Eusuchians now become important, and primitive *Tomistomidae* occur in marine formations both in Europe and in North America. The unique pelican-jawed *Stomatosuchidae* are noteworthy in northern Africa. *Dinosauria* of all groups are still widely distributed, and most of them are highly specialised in various ways. One assemblage of comparatively small and generalised forms in the Danian of Transylvania is considered by Nopcsa to have been isolated from an earlier period on an island. Among *Theropoda* the small *Coeluridae* still occur in Canada and Mongolia, while the *Dinodontidae* are known by fine skeletons in North America and by fragments from Patagonia, New South Wales, Madagascar, N. Africa, and France. The *Ornithomimidae* are also found in both the Old and New World. Among *Sauropoda* the *Titanosauridae*

are specially characteristic of the Upper Cretaceous, and are widely distributed in Europe, India, Madagascar, S. Africa, New Mexico, Brazil, and Patagonia. Of the *Orthopoda*, the *Hypsilophodontidae* survive in North America, and the *Iguanodontidae* are rare in Europe and S. Africa. The more aquatic *Trachodontidae* are abundant, and range from North America to Europe, Siberia, and China. The armoured *Acanthopholidae* and *Nodosauridae*, though best represented in North America, are also found in Europe, S. Africa, and perhaps Argentina. There are primitive Ceratopsians in both North America and Mongolia, and the highly specialised *Ceratopsidae* are exclusively American. The *Pterosauria* are represented only by the *Ornithocheiridae*, which occur in both Europe and North America, and are often toothless and of gigantic size.

At the beginning of the **Tertiary** period, all the characteristic Mesozoic reptiles became extinct, except some rare Mesosuchian *Crocodilia*, which lived in Africa in the Lower Eocene, and certain Rhynchocephalians of the aquatic family *Champsosauridae*, which survived in both North America and Europe until the end of the Lower Eocene. One small lizard-shaped Rhynchocephalian (*Sphenodon*) became isolated in the New Zealand region, where it has lived until the present day. The *Chelonia*, *Lacertilia*, *Ophidia*, and *Crocodilia* had a wider geographical distribution than they have in the existing world, and some of the extinct species are larger than any now living. So far as can be discovered from fragmentary fossils, however, these reptiles have undergone little change since the beginning of the Tertiary period. Large sea-snakes are specially characteristic of the Eocene. Typical leathery turtles (*Dermochelyidae*) range from the Eocene onwards. Until the Miocene, alligators were almost as abundant in Europe as in America, and both alligators and crocodiles lived as far north as central Europe.

Class 4. AVES. Birds.[1]

Feathered, warm-blooded, oviparous vertebrates with chambers of the heart completely separated. A single occipital condyle; the quadrate free. The fore limbs

[1] *Ameghino, F.*, Sur les Oiseaux fossiles de Patagonie. Bol. Inst. Geogr. Argent., vol. xv., p. 501, 1895.—*Beebe, C. W.*, A Tetrapteryx Stage in the Ancestry of Birds. Zoologica (New York Zool. Soc.), vol. ii., no. 2, 1915.—*Beddard, F. E.*, The structure and classification of Birds. London, 1898.—*Fürbringer, M.*, Untersuchungen zur Morphologie und Systematik der Vögel. Amsterdam, 1888.—*Gaillard, C.*, Les Oiseaux des Phosphorites du Quercy. Ann. Univ. Lyon, n.s., Sciences, etc., fasc. 23, 1908.—*Gregory, W. K.*, Theories of the Origin of Birds. Ann. New York Acad. Sci., vol. xxvii., p. 31, 1916.—*Hankin, E. H.*, Development of Animal Flight. Aeronautical Journal, Jan. 1912.—*Heilmann, G.*, The Origin of Birds. London, 1925.—*Huxley, T. H.*, On the classification of Birds. Proc. Zool. Soc., 1867, p. 415.—*Lambrecht, K.*, Geschichte und Bibliographie der Paläo-ornithologie. Aquila (Budapest), vol. xxiii., p. 483, 1916.—Fossilium Catalogus: Aves, 1921.—Fortschritte der Palaeo-Ornithologie. Proc. VII. Internat. Ornithol. Congress, p. 73 1930.—*Lydekker, R.*, Catalogue of fossil birds in the British Museum. London, 1891.—*Marsh, O. C.*, Odontornithes: a monograph of the extinct toothed Birds of North America. Washington, 1880.—*Meyer, A. B.*, Abbildungen von Vogel-Skeleten. Dresden, 1879-90.—*Milne-Edwards, A.*, Recherches anatomiques et paléontologiques pour servir à l'histoire des oiseaux fossiles de la France. Paris, 1867–72.—*Miller, L. H.*, The Birds of Rancho La Brea. Public. Carnegie Inst. Washington, no. 349, art. 5, 1925.—Avian Remains from the Miocene of Lompoc, California. *Ibid.*, 1925.—Also papers chiefly in Bull. Dept. Geol. Univ. Calif., from 1909 onwards.—*Newton, A.*, Dictionary of Birds. London, 1893–96.—*Nopcsa, F.*, Ideas on the Origin of Flight. Proc. Zool. Soc., 1907, p. 223.—Origin of Flight in Birds. *Loc. cit.*, 1923, p. 463.—Noch einmal Proavis. Anat. Anzeig., vol. 67, p. 241, 1929.—*Pycraft, W. P.*, Contributions to the osteology of Birds. Proc. Zool. Soc., 1898–1900.—*Selenka, E.*, and *Gadow, H.*, Aves, in Bronn's Classen und Ordnungen des Thierreichs, 1869–91.—*Shufeldt, R. W.*, Myology of the Raven. London, 1890.—Fossil Birds in the Marsh Collection of Yale University. Trans. Connecticut Acad. Sci., vol. xix., p. 1, 1915.—Also papers in American journals, 1881-1920.—*Wetmore, A.*, Birds of the Past in North America. Smithsonian Report for 1928, p. 377, 1929.—Also papers in American journals, from 1917 onwards.

modified into wings. Proximal tarsals fused with tibia to form a tibio-tarsus; metapodial bones fused with one another, and with the distal tarsals to form a tarso-metatarsus. Fifth digit of the pes always absent.

Of all Classes of vertebrates, birds constitute the most homogeneous and narrowly circumscribed group, and exhibit everywhere the most remarkable uniformity. Descended without question from reptiles, their affinities with that Class are so intimate that Huxley included them both under the common designation of *Sauropsida*. This proposed merging of the two Classes, however, is hardly compatible with such distinguishing characters as the epidermal covering of feathers, heterocoelous vertebrae, and warm blood.

The *exoskeleton* of birds consists of feathers, the horny covering of the beak, claws, and spurs, and certain horny plates often found on the tarsus and feet. Except in penguins, the feathers do not cover the body uniformly, but are arranged in certain definite tracts (*pterylae*), between which are bare spaces (*apteria*). These apteria are best seen on the abdomen and on the sides of the neck in many birds. Although struthious birds are also commonly said to be uniformly covered with feathers, Pycraft has shown the presence of small apteria in most species. Under exceptionally favourable conditions, as in the Lithographic Stone of Bavaria, and the Green River Eocene of Wyoming, imprints of feathers may be preserved in the rocks.

The *skeleton* of birds is remarkable for its combination of compactness and lightness, and for its pneumaticity, or permeation by air cavities. The walls of the bones are very thin, but of dense texture, owing to their richness in calcium phosphate. In young birds the cavities of the long bones are filled with marrow, and this may persist in some bones throughout life, as in several water-birds; on the other hand, the marrow may disappear and the interstices become filled with air, as in the long bones of birds which sail or soar, and many others; finally, the long bones may be completely filled with spongy bone or cancellar tissue, as in penguins. The skull, humerus, and femur are pneumatic in the majority of birds.

The *vertebral column* of birds is divisible into cervical, dorsal, sacral, and caudal regions, but the sacrum or synsacrum of birds is a complex mass of vertebrae not comparable as a whole with the sacrum of other vertebrates. The vertebrae are remarkable for their peculiar saddle-shaped articulations (*heterocoelous*), which allow great freedom of movement. In the Mesozoic *Archaeopteryx* and *Ichthyornis* the centra are slightly amphicoelous, as in modern embryonic birds and in some of the caudal vertebrae of adults. Opisthocoelous vertebrae occur among the dorsals of penguins and a few other birds, such as cormorants and gulls; but the atlas is the only procoelous vertebra in the backbone of birds.

The cervical region (Fig. 519) consists of from thirteen to twenty-five vertebrae, the commonest number being fourteen or fifteen. The centra are mostly elongate and freely movable upon one another, except that in hornbills the atlas and axis may unite, and in a few other birds, the tinamous for example, the last cervical may fuse with the dorsals. The dorsal vertebrae (Fig. 520) number from six to ten, the first of the series being always the first vertebra connected with the sternum by a dorsal and sternal rib. The dorsal series includes also those rib-bearing vertebrae which are united with the sacrum, and the number of free dorsals is much less, being as few as three in *Petroica*, only seven in the long-bodied grebe, and eight

in the crested auklet. The centra of these vertebrae are comparatively short.

In water-birds (*e.g.* penguins and some auks) all the presacral vertebrae may be free, though their motion is restricted; but usually from two to four of the dorsals are fused to stiffen the trunk for flight, one free vertebra being

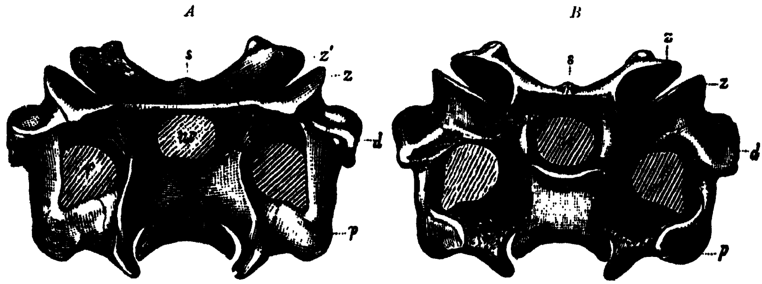


FIG. 519.

Hesperornis regalis Marsh. Upper Cretaceous; Kansas. Anterior (*A*), and posterior (*B*), aspect of thirteenth cervical vertebra. *d*, transverse process; *f*, costal canal for vertebral artery; *nc*, neural canal; *p*, parapophysis; *s*, rudimentary neural spine; *z*, *z'*, anterior and posterior zygapophyses. Nat. size (after Marsh).

left between these and the synsacrum. The latter is a very complex bone, usually composed in the adult of dorsal, lumbar, sacral, and caudal vertebrae united in one solid mass, as many as twenty[1] vertebrae taking part in its formation. The true sacrals are those two lying behind the cavity containing the kidneys, having transverse processes and sacral ribs reaching from their centra to the ilia. The rib-like nautre of these processes may be seen in embryos, particularly of the ostrich, which as well as the apteryx has three sacrals. Most of the vertebrae in the synsacrum are united with the ilia by diapophyses, or transverse processes, given off from the neural arch. The anchylosed vertebrae behind the true sacrals are the urosacrals, and belong to the caudal series; their number may vary slightly within specific limits. The free caudals in existing birds usually number about six, besides the terminal ploughshare-bone or pygostyle, which is composed of from four to six fused vertebrae. In the Jurassic *Archaeopteryx* there were at least twenty free and long caudals with a pair of rectrices to each vertebra.

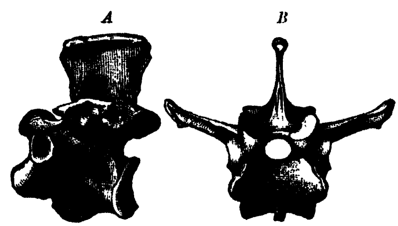


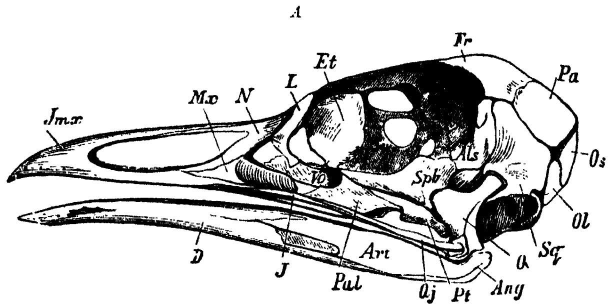
FIG. 520.

Hesperornis regalis Marsh. Upper Cretaceous; Kansas. Lateral (*A*), and anterior (*B*), aspects of dorsal vertebra. $1/2$ nat. size (after Marsh).

All the presacral vertebrae except the atlas usually bear ribs which may be present also on the anterior two or three sacrals; those of the cervical region fuse with the vertebrae, except the last two or three. The true character of the cervical processes thus formed may be seen in embryos, especially in the young ostrich, where they remain for some time free, as they did permanently in *Archaeopteryx*. Nearly always the last cervical rib and all the thoracic ribs except the last one or two bear an uncinate process, or thin flat blade of bone directed obliquely upward and backward to overlap the succeeding rib. These processes usually unite with the ribs, but in some

cases (Moas and many water-birds) they remain free. They are absent in the screamers, *Chauna* and *Palamedea*, while they are vestigial in the secretary bird. Appended to the thoracic ribs are sternal ribs, from two to five pairs of which are attached to the sternum.

A *sternum* is always present, and this is externally convex and generally broad. It may cover only the anterior portion of the thorax, or may be so prolonged, as in water-birds, that its posterior end underlies the pelvis, or extends nearly to the pubes, as in humming-birds. In birds of flight or those which use their wings in swimming, as the penguins and auks, the sternum is keeled beneath; but in flightless birds (Ratites) it may be without keel. The anterior end may or may not bear a manubrial process, the posterior portion may be pointed, rounded, emarginate, or have two or four



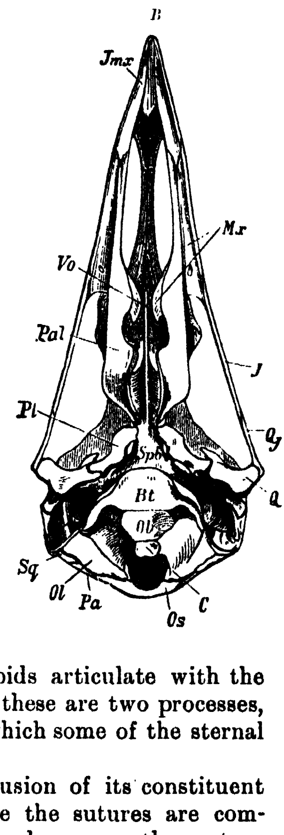


FIG. 521.

Otis tarda Linn. Recent; Europe. Lateral (*A*), and palatal (*B*), aspects of skull, 1/1. *als*, alisphenoid; *ang*, angular; *art*, articular; *bt*, basitemporal; *c*, occipital condyle, underneath foramen magnum; *d*, dentary; *et*, median ethmoid; *fr*, frontal; *j*, jugal; *jmx*, premaxilla; *l*, lachrymal; *mx*, maxilla; *N*, external nares: *ob*, basioccipital; *ol*, exoccipital; *os*, supraoccipital; *pa*, parietal; *pal*, palatine; *pt*, pterygoid; *q*, quadrate; *q.j*, quadrato-jugal; *sm*, interorbital septum; *spb*, basisphenoid; *sq*, squamosal; *vo*, vomer (after Claus).

notches, which are sometimes very deep. The coracoids articulate with the front portion of the sternum, and immediately behind these are two processes, one on either side, known as the costal processes, to which some of the sternal ribs are articulated.

The *skull* (Fig. 521) is characterised by the early fusion of its constituent bones, especially those forming the brain-case where the sutures are completely obliterated in the adult. In the tinamous, however, the suture between the parietals and frontals seems to remain permanently open. The brain-cavity is larger than in reptiles, much exceeding that even of Pterosaurs. The cranial osteology is very similar to that of the *Diapsida* or *Archosauria*, the chief difference consisting in the constant absence of an upper and presence of a lower temporal arch. The large orbits look forward in the owls, but are laterally directed in the majority of birds, and except in parrots are incompletely enclosed on the inferior margin. A sclerotic ring of numerous bony pieces is very generally developed round the eye. An antorbital vacuity is present, as in Dinosaurs, Pterosaurs, and Crocodilians, close in front of which, near the base of the beak, are placed the paired external narial openings.

The single occipital condyle, formed mainly by the basioccipital, is directed downwards and forwards so that the long axis of the head is approximately at right angles to that of the neck. The paired parietals are smaller than the large frontals, which form the greater part of the cranial roof and upper border of the orbits. Independent postorbitals and postfrontals are not developed. The inferior temporal arch, formed by the slender jugal and quadrato-jugal, connects the equally slender maxilla with the quadrate.

The squamosal and periotic elements (proötic, epiotic, and opisthotic) fuse to form a single bone which is united with the occipital and parietals, and to which the large quadrate is movably attached. An independent lachrymal is often present at the anterior margin of the orbit, and there is an ossified or membranous interorbital septum of considerable size. In the anterior prolongation of the latter is a vertically placed unpaired ethmoid, which is continued in front as a bony or cartilaginous nasal septum. The lateral ethmoids are placed between the orbits and external nares, and are pierced for the passage of the olfactory nerves. The greater part of the beak is formed by the fused premaxillae, with the sides of which the maxillae are fused; its margins are sheathed with a horny layer, and it is often movably connected with the skull. When the mouth is opened, the end of the beak is raised by pressure transmitted to it from the quadrate by means of the pterygoid and palatine bones, and more especially by the rod-like quadrato-jugal.

The bones of the palatal portion of the skull are arranged on two plans. In the one the vomer is broad and unites in front with the maxillo-palatines, while behind it receives the posterior extremities of the palatines and the anterior ends of the pterygoids, which are usually excluded from contact with the sphenoidal rostrum. This is the *dromaeognathous* or *palaeognathous* type of palate found in struthious birds, the apteryges and tinamous. In birds with this arrangement the head of the quadrate usually has only a single articular face, or is but faintly divided into two portions; and rather long basipterygoid processes from the sides of the sphenoid give this bone a somewhat-cruciform shape.

In the second type of palate, which may be called the *euornithic* or *neognathous*, the vomer embraces posteriorly the sphenoidal rostrum between the palatines, and these latter articulate with the pterygoids and with the rostrum. This arrangement occurs in the large majority of birds, and they also have the head of the quadrate double, or with two articular facets. Basipterygoid processes are present in some euornithic skulls, but these most frequently assume the form of low facets on the sphenoidal rostrum, with which the pterygoids are movably articulated. The euornithic type of skull is subject to various modifications in the development of the vomer and those inwardly directed processes of the maxillae termed the maxillo-palatines. When the vomer is pointed in front and entirely free from the maxillo-palatines, and these are free from each other, the skull is termed *schizognathous*; when the maxillo-palatines are expanded and fused with each other, the vomer being small or absent, the skull is *desmognathous*; when the vomer is expanded in front and free from the maxillo-palatines, and these are slender at their point of origin and disjoined, the skull is said to be *aegithognathous*.

The bones bounding the narial openings are arranged in one of two ways, named *holorhinal* and *schizorhinal*. In the holorhinal type the openings are

more or less oval, the posterior border curved and lying in advance of the posterior ends of the premaxillae. In the schizorhinal type the openings are more or less elongate with the posterior border angular or slit-like and lying behind the posterior ends of the premaxillae.

In all modern birds the mandibular rami become fused at an early stage into a long symphysis, and only among certain Mesozoic forms (*Ichthyornis*) are they united by suture or by ligaments as in reptiles. The six elements of which the mandible is composed fuse into a single piece, and there is frequently a lateral vacuity behind the dentary and splenial, as in crocodiles. Although the earliest known birds have conical teeth in sockets, and dental papillae or a dental ridge sometimes occur in the jaws of some modern embryos (parrot, ostrich), true teeth are invariably wanting among existing species.

The *pectoral arch* is firmly attached to the thorax to facilitate flight. The long blade-like scapula has no ridge, extends along the dorsal side of the thoracic ribs, and takes part with the coracoid in the glenoid cavity for the head of the humerus. Penguins are exceptional in having the scapula broadly expanded posteriorly. The coracoids are stout and pillar-like, their function being to receive the downward pull of the wing-muscles during flight. The clavicles, which are usually united in a forked bone (*furcula*), sometimes act as supports; and by their union with the coracoids at the shoulder-joint, and with the sternal keel below in the centre, tend to resist the thrust of the wing-muscles in flight. In some birds of powerful flight (pigeons, humming-birds), however, the clavicles are so weak as to be of no mechanical service. Among Ratites and also a few Carinates (toucans, parrots) the clavicles are vestigial or wanting, and never unite to form a furcula. The furcula of Carinates may anchylose either with the keel of the sternum (*Steganopodes*) or with the coracoids (*Opisthocomus*), and in the frigate birds with both at once.

The humerus of Carinates is expanded at both ends, and provided at its proximal extremity with a strong pre-axial delto-pectoral ridge for the attachment of the pectoral muscles. Its articular head is vertically elongated, and there is often a pneumatic foramen adjoining it on the inner side. At its distal extremity is a prominent oblique condyle on the inner side of the palmar aspect for articulation with the radius, but there are never any condylar foramina. The humerus of flightless birds is degenerate, and sometimes even absent, as in many Moas. In the fore wing, which is generally longer than the humerus, the ulna is more strongly developed than the radius, and often exhibits a row of tubercles along its lower edge for the attachment of the secondaries. The carpus of adult modern birds contains only two bones (radiale and ulnare); a distal row, however, is indicated in embryos by two separate cartilaginous elements, which later become fused with the metacarpals. The latter are never more than three in number, are unequally developed, and in existing Carinates are more or less completely fused. Metacarpal no. I is much reduced, and bears one or more, rarely two, short phalanges for the support of the so-called bastard wing (*alula*); the second metacarpal usually bears two phalanges and the third, one. The first and second digits are sometimes clawed (*Struthio*, *Rhea*, *Chauna*), and in *Archaeopteryx* all three terminate in claws.

The three elements of the *pelvis* are anchylosed (except in *Archaeopteryx*), and usually unite with the synsacrum. In water-birds this union takes place somewhat slowly, and in penguins and the great auk not at all. The ilium

is elongate, and may, as in birds of prey, extend much further in front of the acetabulum than behind it. Ischium and pubis are both directed backwards. The pubes often remain free from the ischia, and never unite with one another to form a symphysis except in *Archaeopteryx* and the ostrich. Since the retroversion of the pubis is proved by embryological researches to be a secondary modification, no homology can exist between this and the postpubis of Orthopodous Dinosaurs, and the *processus iliopectinealis* (Fig. 522) must be regarded as a structure peculiar to birds alone.

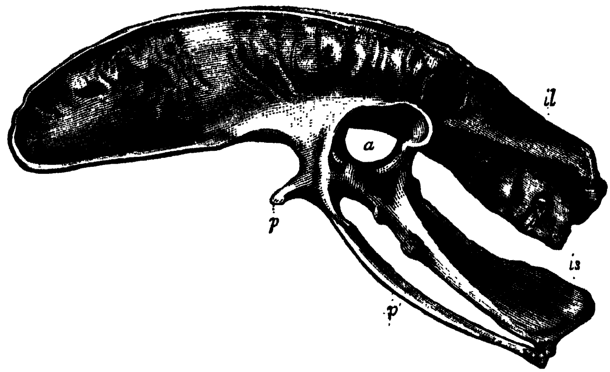


FIG. 522.
Apteryx australis Owen. Recent; New Zealand. Left lateral aspect of pelvis. *a*, acetabulum; *il*, ilium; *is*, ischium; *p*, ilio-pectineal process; *p'*, pubis. 3/4 nat. size (after Marsh).

FIG. 523.
Meleagris gallipavo Linn. Anterior (*A*), and proximal (*B*), aspect of tarso-metatarsus of young individual.

The femur in birds is short and stout, with the neck and head extending inwards into the acetabulum at right angles to the shaft. The latter is directed forwards and slightly downwards during life, and is concealed beneath the flesh and feathers of the abdomen in such a way that the knee-joint is not visible externally. Its distal condyles are large and antero-posteriorly elongated, and a patella is present in most cases. The tibia is a stout bone considerably longer than the femur. Its expanded proximal end exhibits a procnemial crest, which may extend above the knee-joint; and the distal extremity has a trochlea-like surface, transversely elongated, and slightly hollowed in the middle. In young Ratites, and in the embryos of Carinate birds, the presence of a suture near the distal end of this bone indicates that an astragalus and calcaneum are fused with it, thus forming a tibio-tarsus. In the Moas the united astragalus and calcaneum remain for some time free from the tibia.

The fibula in birds is a degenerate bone, and best developed in the Moas, where, although short, it is stout and free. In most birds it is more or less fused with the tibia, and is longest in the penguins, the fish-hawk, and some owls, where it reaches almost to the ankle-joint.

The distal row of tarsals fuses with the coössified metatarsals to form a tarso-metatarsus (Fig. 523). This bone is peculiarly characteristic of birds, and its variations, together with those of the tibia, cause the differences in the length of the leg among different forms, which are sometimes enormous. The fifth metatarsal is never developed, and the first, when present, is always reduced,

being attached to the inner side of the tarso-metatarsus by ligament, or more rarely by suture. Metatarsals nos. II to IV are imperfectly united in *Archaeopteryx*, and completely separated in the embryos of modern birds; but in the adult they are always fused into a single bone, although the three components are plainly distinguishable in penguins. This metapodial element terminates distally in three pulley-like surfaces for the articulation of the phalangeals. Generally the median condyle is thrust forward in advance of the other two, and the modifications of this region afford important taxonomic characters. There is remarkable constancy in the number of phalanges in the toes of birds, the formula being 2, 3, 4, 5 in almost all cases where the full complement of digits is present. The hallux, however, is frequently wanting, and in the ostrich only digits nos. III and IV are developed. An apparent exception to the usual formula occurs among some swifts and goatsuckers, where owing to fusion of some of the phalanges the formula is 2, 3, 3, 3.

Fossil egg-shells or casts of the same have been obtained from the Cretaceous and various Tertiary horizons, but are naturally much less common than bones of the skeleton. They belong for the most part to cursorial or wading birds. The largest known eggs are those of *Aepyornis*, from the superficial deposits of Madagascar, which have a capacity of about eight litres. Foetal bones are occasionally found in Moa eggs from New Zealand. Footprints of birds are extremely rare. Those of the Moa have been found on old sandy beaches in New Zealand, and some three-toed footprints on the Lithographic Stone of Bavaria may have been made by *Archaeopteryx*.

In comparison with the large number of recent species of birds, the known fossil forms are few, and most of them are represented by such imperfect fragments that the determination of their affinities is difficult. So far as the record can be interpreted, nearly all the birds of the Tertiary period were essentially like those of the present day, only sometimes differently distributed. The few known Mesozoic birds, however, were in several respects more primitive. In the Jurassic *Archaeopteryx*, the oldest known bird, the tail had not become atrophied, and the teeth were not lost in the adult; the pelvis was not fully developed, and the vertebrae had not yet acquired the saddle-shaped articulations characteristic of nearly all post-Jurassic forms.

The scarcity of the fossil remains of birds is explained by the mode of life of most of them and their alertness in avoiding danger. Exceptional accumulations of their bones occur in various cave and fissure deposits (such as the Oligocene Phosphorites of Quercy, France), in some lake deposits (such as those of Allier, France, and Fossil Lake, Oregon), and in river deposits (such as in Santa Cruz, Patagonia). Their remains are also numerous in the asphalt of Rancho La Brea, California, which has trapped birds and mammals since the Pleistocene period; in the swamps of Madagascar and New Zealand; and in the cooking-places of the Aborigines of New Zealand. A few birds have even been preserved whole by saturation with petroleum in a marsh at Starunia, Galicia, near the Carpathian mountains.

The existing birds are usually classified in two great groups, the *Ratitae* and *Carinatae*, the former comprising the ostrich-like running birds with a flat sternum, the latter the rest of the birds with a keeled sternum (unless degenerate) and well-developed muscles for flight. The *Crypturi* were removed from the *Carinatae* by Stejneger and also by Pycraft, who classified

them with the *Ratitae* in a division named *Palaeognathae*, while the remaining carinates formed the *Neognathae*. Stejneger and Fürbringer especially contributed to a more satisfactory classification, and F. A. Lucas, in the last English edition of this Text-book (1902), based on their conclusions the arrangement which is adopted, with slight modifications, in the following pages.

Sub-Class 1. SAURURAE.[1]

Tail feathers arranged in pairs, one on either side of each vertebra in an elongated tail. Vertebrae amphicoelous; cervical ribs free; dorsal ribs without uncinate processes. Abdominal ribs present. Pelvic bones separate. Metacarpals separate. Each digit with a claw.

Order 1. ARCHAEORNITHES.

Skull typically bird-like, with a series of conical teeth in sockets along the margin of the jaws. The lizard-like tail longer than the presacral portion of the vertebral column. Remiges and rectrices, with their coverts, well developed. Upper Jurassic.

FIG. 524.

Archaeopteryx siemensi Dames. Lithographic Stone; Eichstadt, Bavaria. *c*, carpal; *cl*, furcula; *co*, coracoid; *h*, humerus; *r*, radius; *sc*, scapula; *u*, ulna. Original in Berlin Museum. 2/7 nat. size (from Steinmann and Döderlein.)

Archaeopteryx H. von Meyer (*Gryphosaurus* Wagner; *Archaeornis* Petronievics) (Fig. 524). This primitive bird is known so far only by three specimens from

[1] *Dames, W.*, Ueber *Archaeopteryx*. Palaeont. Abhandl., vol. ii., p. 119, 1884.—Über Brustbein, Schulter- und Beckengürtel der *Archaeopteryx*. Sitzungsber. k. preuss. Akad. Wiss, vol. xxxviii., p. 818, 1897.—*Edinger, T.*, Brain of *Archaeopteryx*. Ann. Mag. Nat. Hist. [9], vol. xviii., p. 151, 1926.—*Jaekel, O.*, Die Spur eines neuen Urvogels (*Protornis bavarica*). Palaeont. Zeitschr., vol. xi., p. 201, 1929.—*Nopcsa, F.*, Bemerkungen zu Petronievics seinen Arbeiten über *Archaeopteryx*. Ann. Géol. Pénin. Balkan., vol. viii., p. 105, 1926.—*Owen, R.*, On the *Archaeopteryx* of von Meyer. Phil. Trans., vol. cliii., p. 33, 1863.—*Petronievics, B.*, Über das Becken, etc., der Londoner *Archaeopteryx*. Geneva, 1921.—Über die Berliner *Archaeornis*. Geneva, 1925.—Nouvelles Recherches sur l'ostéologie des *Archaeornithes*. Ann. Paléont., vol. xvi., p. 39, 1928.—Zur Pubisfrage der *Archaeornis*. Anat. Anzeig., vol. lxv., p. 342, 1928.—*Petronievics, B.*, and *Woodward, A. S.*, Pectoral and Pelvic Arches of *Archaeopteryx*. Proc. Zool. Soc., 1917, p. 1.—*Pycraft, W. P.*, The Wing of *Archaeopteryx*. Nat. Sci., vol. viii., p. 261, 1896.—*Seeley, H. G.*, Professor C. Vogt on *Archaeopteryx*. Geol. Mag. [2], vol. viii., p. 454, 1881.

the Lithographic Stone of Bavaria—an isolated feather in the Palaeontological Museum, Munich, a skeleton without head and neck in the British Museum, and a skeleton including both these parts in the Berlin Museum. The two skeletons are generally considered as representing two species, *A. macrura* and *A. siemensi*, and they are regarded by Petronievics as belonging to two distinct genera and families. The one skeleton fortunately supplements the other so that the osteology is well known. Contrary to the usual condition among birds, none of the bones appear to have been pneumatic.

The skull is shaped like that of a typical bird, its constituent elements being fused together, and the quadrate apparently free. A sclerotic ring is present. There is a series of thirteen conical teeth on each side in the upper jaw, fixed probably in distinct sockets; there are also similar teeth in the lower jaw. The vertebral column comprises about fifty vertebrae, of which ten or eleven are cervical, eleven or twelve dorsal, two lumbar, seven or eight sacral, and about twenty caudal. The cervical and dorsal vertebrae seem to have been amphicoelous or amphiplatyan, and bear weakly developed transverse processes and neural spines. The ribs are very slender, free in the neck region, and without ossified uncinate processes in the thoracic region. Twelve or thirteen pairs of abdominal ribs are present in the ventral wall of the body cavity. In the pectoral arch the long and slender scapula is essentially bird-like, and exhibits a well-developed acromion. The sternum is not known, but the coracoids and U-shaped furcula resemble those of modern birds. The wing is relatively small, and its bones are slender. Radius and ulna are straight, and little shorter that the humerus. The carpus is imperfectly known, and the three metacarpals appear to have been free. Metacarpal no. I is short, and no. II longer and stouter than the first or third. The manus terminates in three clawed digits having the phalangeal formula 2, 3, 4.

The three pelvic elements appear to have articulated with each other by persistent sutures. The acetabulum is perforate. The long and slender pubes meet distally in an elongated symphysis, and each is pierced at the upper end by a small obturator foramen. The hind limb is essentially avian, and notable only for the weak development of the cnemial crest of the tibia. There are four clawed digits in the pes (nos. I to IV), with the phalangeal formula 2, 3, 4, 5. In the wing are observed seven primary and ten secondary remiges with their coverts. The rectrices of the tail are arranged in pairs, directed obliquely backward, one pair to each vertebra. Contour feathers are also indicated on the neck and along the tibia.

The two known species of *Archaeopteryx* are about as large as an ordinary domestic fowl, and must have been capable of flight. The clawed digits of the manus were doubtless useful for climbing trees and rocks. Some three-toed footprints in the Lithographic Stone of Solenhofen, associated with a groove left by the tail, have been ascribed to *Archaeopteryx* by Oppel. Other footprints from the same formation are referred by Jaekel to allied birds which he names *Protornis* and *Hypornithes*.

The fragmentary crushed skull from the Upper Jurassic (Morrison Formation) of Wyoming, U.S.A., described as *Laopteryx* Marsh, may be reptilian.

Sub-Class 2. ORNITHURAE.

Tail feathers arranged like a fan round the end of the shortened tail, of which several terminal vertebrae are usually fused in a pygostyle. Vertebrae very rarely

FIG. 525.

Hesperornis regalis Marsh. Upper Cretaceous; Kansas. Restoration of skeleton. $^1/_8$ nat. size (after Marsh). The bird would probably not be able to stand upright in the attitude here shown, the hind limbs being too much adapted for swimming.

amphicoelous, usually with saddle-shaped articulations; cervical ribs fused with centra; dorsal ribs with uncinate processes (except in Palamedea and Chauna). Pelvic bones proximally united. Metacarpals united.

Order 1. ODONTOLCAE.[1]

Birds with teeth implanted in a continuous groove. Bones of cranium usually fused, but those of mandible separate; basipterygoid processes absent; a pair of

[1] *Lambrecht, K.*, *Neogaeornis wetzeli* n.g., n.sp., der erste Kreidevogel der südlichen Hemisphäre. Palaeont. Zeitschr., vol. xi., p. 121, 1929.—*Lucas, F. A.*, Osteology and Relationship of

vomers; quadrate single-headed; mandibular rami not fused at symphysis. Clavicles not united in a furcula. Pelvic bones free distally. Upper Cretaceous.

The family *Hesperornithidae* is known by nearly complete skeletons of *Hesperornis* from the marine Niobrara Cretaceous of Kansas, U.S.A.

Hesperornis Marsh (*Coniornis* Marsh) (Figs. 519, 520, 525). Snout much elongated; premaxilla toothless, but a regular row of teeth in the maxilla and in the mandible as far forwards as the symphysis. The proximal articulation of the quadrate is slightly divided into two facets of unequal size. The articulations of the vertebrae are saddle-shaped. There are twenty-three presacral vertebrae and fourteen vertebrae in the sacrum. The coracoid is short and very broad, and the sternum is without a keel. Of the wing, only the much reduced humerus is known. The pelvis is laterally compressed, and the hind limbs are as completely adapted for swimming as in the existing *Colymbidae*. The patella is very large, and the fourth or outer toe of the foot is much the largest, being nearly twice the length of the third toe. The feathers seem to have extended even over the tarsus. *H. regalis* Marsh, with skeleton over a metre in length. Upper Cretaceous; Kansas. Fragments of other species in Kansas and Montana (Claggett Formation).

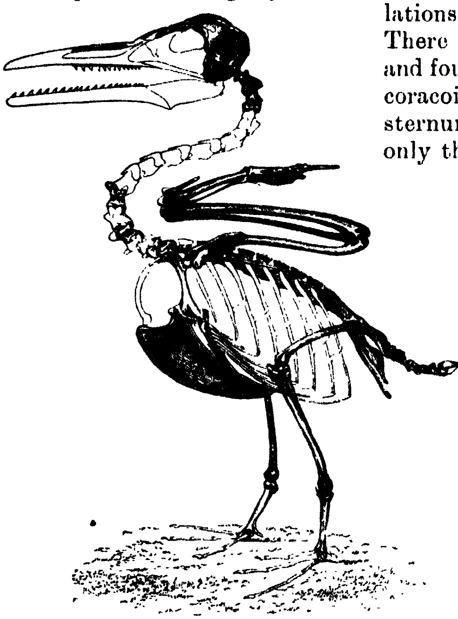


FIG. 526.
Ichthyornis victor Marsh. Upper Cretaceous; Kansas. Restoration of skeleton. $^1/_2$ nat. size (after Marsh).

Baptornis Marsh; *Hargeria* Lucas. Niobrara Cretaceous; Kansas.

Enaliornis Seeley. Fragments from the Cambridge Greensand.

Neogaeornis Lambrecht. Tarsometatarsus from Upper Cretaceous (Quiriquina Formation) of southern Chile.

Order 2. ODONTORMAE.

Birds with teeth in separate sockets and with slightly amphicoelous vertebrae Quadrate single-headed. Mandibular rami not fused at symphysis. Pelvic bones free distally. Upper Cretaceous.

The *Ichthyornithidae* comprise small flying birds with a very deep keel on the sternum, known chiefly from the marine Niobrara Cretaceous of Kansas.

the Fossil Birds of the Genera *Hesperornis*, *Hargeria*, *Baptornis*, and *Diatryma*. Proc. U.S. Nat. Mus., vol. xxvi., p. 545, 1903.—*Lull, R. S.*, Organic Evolution (New York, 1922), pl. xv. [photographs of *Hesperornis* in Peabody Museum].—*Marsh, O. C.*. Odontornithes. Washington 1880.—*Seeley, H. G.*, British Fossil Cretaceous Birds. Quart. Journ. Geol. Soc., vol. xxxii. p. 496, 1876.—*Shufeldt, R. W.*, Base of the Cranium of *Hesperornis regalis*. Bull. Amer. Palaeont. vol. v., p. 75, 1915.—Fossil Remains of *Hesperornis* found in Montana. The Auk, vol. xxxii. p. 290, 1915.—*Williston, S. W.*, Plumage of *Hesperornis*. Kansas Univ. Quart., vol. v. p. 53, 1896.

Ichthyornis Marsh (Figs. 526-528). Bones delicate and more or less pneumatic. Cranial bones fused. Snout elongated, the premaxilla probably toothless, but the maxilla and mandible with a regular series of teeth, which have vertical successors. Sacrum with ten vertebrae; five caudal vertebrae and

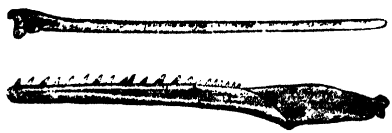


FIG. 527.
Ichthyornis dispar Marsh. Upper Cretaceous; Kansas. Mandible. 3/4 nat. size (after Marsh).

FIG. 528.
Ichthyornis dispar Marsh. Lateral (*A*), and anterior (*B*), aspect of cervical vertebra. 2/1 nat. size (after Marsh).

a small pygostyle. The pelvic bones are fused. *I. victor* Marsh, about as large as a pigeon. This and other species in the Upper Cretaceous of Kansas.

Apatornis Marsh. Niobrara Cretaceous; Kansas.

? *Cimolopteryx* Marsh. Laramie (Lance) Formation; Wyoming.

Order 3. DROMAEOGNATHAE.[1] (*Palaeognathae.*)

Toothless birds. Vomer broad and united in front with the maxillo-palatines, behind with the pterygoids; pterygoids usually not in contact with the sphenoidal rostrum; quadrate single-headed; mandibular rami fused at symphysis. Ischia slender and free at the distal end or only united with the ilia. Upper half of tarso-metatarsus usually without canal for passage of tendon. Terminal caudal vertebrae rarely forming a pygostyle.

The *Dromaeognathae* are the scattered survivors of the ancient avi-fauna of the globe, and some are confined to a remarkably small area. Greater differences of structure are to be found among the few members of this division than among all other existing birds, and these differences are such that they are frequently placed in different Orders. The flightless struthious birds have a keel-less sternum which is very variable in shape posteriorly, while the shoulder girdle exhibits various degrees of degeneration from the absence of clavicles to the lack of the entire wing. The ischia and pubes in the pelvis are also very variable.

Sub-Order 1. STRUTHIONES.

This Sub-Order is represented in the existing world by the ostriches (*Struthio*), rheas (*Rhea*), cassowaries and emeus (*Casuarius* and *Dromaeus*), these forming three families. It also includes the extinct *Aepyornithidae* of Madagascar and the *Dinornithidae* or Moas of New Zealand. They are all large flightless birds, having a typically dromaeognathous skull with the long basipterygoid processes arising from the body of the basisphenoid, giving it something of a cruciform shape; the nostrils are holorhinal. The sternum is not keeled; the scapula and coracoid are short and fused with one another, and the wings are

[1] *Pycraft, W. P.*, Morphology and Phylogeny of the *Palaeognathae* (*Ratitae* and *Crypturi*) and *Neognathae* (*Carinatae*). Trans. Zool. Soc., vol. xv., p. 149, 1900.

small or vestigial. These are characters correlated with loss of the power of flight.

Family 1. **Struthionidae.**[1]

In the *Struthionidae*, or ostriches, the pubes are united in a ventral symphysis, and the toes are reduced to two, the third and fourth digits only being present, and the weight of the body carried mainly by the third, a specialisation for running. Fossil remains of these birds occur in the Upper Pliocene of the Siwalik Hills (India), and in the Lower Pliocene of the Island of Samos, southern Russia (near Odessa), Persia, Mongolia, and northern China, while fossil eggs, slightly larger than those of the living ostrich, have been described under the name of *Struthiolithus* Brandt, from superficial deposits of southern Russia and northern China. Fragments of similar eggs occur in Palaeolithic hearths in Ordos, China. Other fragments of egg-shell have been found in superficial deposits in northern India.

Family 2. **Rheidae.**[2]

The rheas (*Rhea* Brisson) have the ischia turned inward, so that they meet and are united beneath the ilia, while some of the anterior caudal vertebrae are atrophied. There are three digits in the foot. The species of this family are confined to southern South America. Remains of *Rhea* itself occur in the Pleistocene (Pampean) deposits of Argentina. *Protorhea* Moreno and Mercerat, with a stouter femur which has a relatively small trochanter, is found in the Lower Pleistocene of Monte Hermoso, Argentina. *Heterorhea* Rovereto, also from Monte Hermoso.

Family 3. **Dromaeidae.**[3]

The emeus (*Dromaeus* Vieillot) from Australia, and the cassowaries (*Casuarius* Brisson) from Northern Australia and some islands to the northward, are three-toed. The bones of the wing are greatly reduced in size. Fossil remains of both genera are found in the Wellington caves, New South Wales. The extinct genus *Genyornis* Stirling and Zietz, from the Pleistocene of Lake Callabonna, South Australia, has the lower jaw unusually large, and digit II of the hind foot comparatively small and slender. In *G. newtoni* S. and Z. the skull is about 30 cm. long, and the tibio-tarsus about 60 cm. long. *Dromornis* Owen, known by fragments from the Pleistocene and presumed Pliocene of Australia, may be another extinct genus of the same family. *Hypselornis* Lydekker is known by a phalangeal bone from the Pliocene of India.

[1] *Andersson, J. G.*, Fossil Remains of *Struthionidae* in China. Mem. Geol. Surv. China, ser. A., no. 3, p. 53, 1923.—*Bensley, B. A.*, Egg of *Struthiolithus chersonensis* Brandt. Univ. Toronto Studies, Biol. Ser. no. 19, 1921.—*Bidwell, E.*, Egg-shell of Indian Ostrich. Ibis, 1910, p. 759.—*Eastman, C. R.*, *Struthiolithus chersonensis* from Northern China. Bull. Mus. Comp. Zool. Harvard, vol. xxxii., p. 127, 1898.—*Lowe, P. R*, Phylogeny of the Ostrich and its Allies. Proc. Zool. Soc., 1928, p. 185.—Struthious Remains from China and Mongolia. Palaeont. Sinica, ser. C, vol. vi., fasc. 4, 1931.—*Martin, R.*, Remains of *Struthio karatheodoris* Major of the Island of Samos. Proc. Zool. Soc., 1903, vol. i., p. 203.

[2] *Moreno, F. P.*, and *Mercerat, A.*, Pájaros Fósiles de la República Argentina. Anales Mus. La Plata—Paleont. Argent., vol. i., p. 7, 1891.

[3] *Owen, R.*, *Dromornis australis* Owen. Trans. Zool. Soc., vol. viii., p. 381, 1873.—*Stirling, E. C.*, and *Zietz, A. H. C.*, *Genyornis newtoni.* Mem. Roy. Soc. S. Australia, vol. i., p. 43, 1900.

Family 4. **Aepyornithidae.**[1]

The *Aepyornithidae*, although known only by fossil remains, including egg-shells, from Madagascar, have become extinct at a comparatively recent epoch. They were birds of great size and massive build, having a relatively small skull and an unusually short and broad sternum, with well-developed facets for the coracoids. Foot normally with four digits, but the hallux sometimes wanting. Their nearest relatives are considered to be the cassowaries and emeus. The typical species is *Aepyornis maximus* Geoffroy, which is considerably exceeded in size by *A. titan* Andrews, with a tibio-tarsus 80 cm. in length. *Müllerornis* Milne Edwards (*Flacourtia* Andrews) is represented by smaller species.

According to K. Lambrecht, the following fragments suggest that this family originated in Africa. A distal end of tibio-tarsus (*Eremopezus eocaenus* Andrews) and part of a tarso-metatarsus (*Stromeria fajumensis* Lambrecht) from the Lower Oligocene of the Fayum, Egypt; portions of egg-shell (*Psammornis rothschildi* Andrews) from the Eocene of Touggourt, southern Algeria.

Family 5. **Dinornithidae.**[2]

In the *Dinornithidae* or "Moas" the wings and pectoral arch are extremely rudimentary or absent. The beak short and slightly deflected. The hind limbs in most species are exceptionally massive. The femur is usually without pneumatic foramina, and the tibio-tarsus has a bony bridge over the groove for extensor tendons. The hallux is sometimes present in addition to the three usual digits.

The "Moas" were restricted to New Zealand, where they lived in great abundance and variety during the Pleistocene period, and only became extinct in comparatively modern times. The oldest known remains are a few bones from a Pliocene formation. Numerous bones have been found in swamps, and both bones and egg-shells occur in the refuse heaps of the Maoris. A few complete skeletons are known from fissures and caves, and some fragments from very dry fissures exhibit ligaments, skin, and feathers.

[1] *Andrews, C. W.*, New Species of *Aepyornis* (*A. titan*). Geol. Mag. [4], vol. i., p. 18, 1894.—Nearly complete Skeleton of *Aepyornis*. *Loc. cit.*, vol. iv., p. 241, 1897.—Skull, Sternum, and Shoulder-Girdle of *Aepyornis*. Ibis, 1896, p. 376.—Pelvis and Hind-limb of *Mullerornis betsilei*. . . . Occurrence of a Ratite Bird in the Upper Eocene Beds of the Fayum, Egypt. Proc. Zool. Soc., 1904, p. 163.—Fragments of the Fossil Egg-shell of a large Struthious Bird from Southern Algeria. Bericht V Internat. Ornithol. Kongrez, Berlin, p. 169, 1910.—*Burckhardt, R.*, Über *Aepyornis*. Palaeont. Abhandl., n.f., vol. ii., p. 145, 1893.—*Capellini, G.*, Uovo di *Aepyornis maximus*. Mem. R. Accad. Sci. Bologna [4], vol. x., p. 23, 1889.—*Grandidier, G.*, *Aepyornis* de Madagascar. Comptes rendus Acad. Sci. Paris, vol. 137, p. 208, 1903.—*Lambrecht, K.*, *Stromeria fajumensis* n.g., n.sp. Abhandl. Bay. Akad. Wiss., math.-naturw. Abt., n.f., vol. iv., p. 1, 1929.—*Lowe, P. R.*, Relationships of the *Aepyornithes* to other *Struthiones*. Ibis, 1930, p. 470.—*Monnier, L.*, Les *Aepyornis*. Ann. Paléont., vol. viii., p. 125, 1913.

[2] *Andrews, C. W.*, Complete Skeleton of *Megalapteryx tenuipes* Lydekker in the Tring Museum. Novitates Zoologicae, vol. iv., p. 188, 1897.—Nearly complete Skeleton of *Dinornis maximus*. Geol. Mag. [4], vol. vi., p. 395, 1899.—*Hamilton, A.*, Bibliography of *Dinornithidae*. Trans. New Zealand Inst., vol. xxvi., p. 229, 1893.—*Hutton, F. W.*, Moas of New Zealand. *Loc. cit.*, vol. xxiv., p. 93, 1891; also vol. xxv., p. 6, 1892.—*Owen, R.*, Memoirs in Trans. Zool. Soc., vols. iii., iv., v., vii., x., xi., 1846–82; reprinted with additions in a volume, Memoirs on the Extinct Wingless Birds of New Zealand. London, 1879.—*Parker, T. J.*, Cranial Osteology, Classification, and Phylogeny of the *Dinornithidae*. Trans. Zool. Soc., vol. xiii., p. 373, 1895.

The feathers bear a large aftershaft, like the feathers of the emeus and cassowaries. Bony tracheal rings are often found. Gizzard stones have also been noticed, and coprolites show that the birds fed on ferns.

Dinornis Owen (*Movia* Reichenbach; *Tylopteryx* Hutton). Beak relatively wide and pointed, temporal fossae large. About twenty vertebrae in cervical and sacral regions respectively. Sternum about as long as broad, very convex, with small coracoidal facets, three costal facets on each side, widely divergent lateral processes, and a xiphisternal notch. Scapulo-coracoid element without glenoid cavity for the humerus. Pelvis with much elevated ilium. Femur comparatively long, its medullary cavity with very thick walls. Tibio-tarsus and tarso-metatarsus also long and slender; hallux reduced or absent. *D. maximus* Owen attained a height of over 3·5 m. when standing.

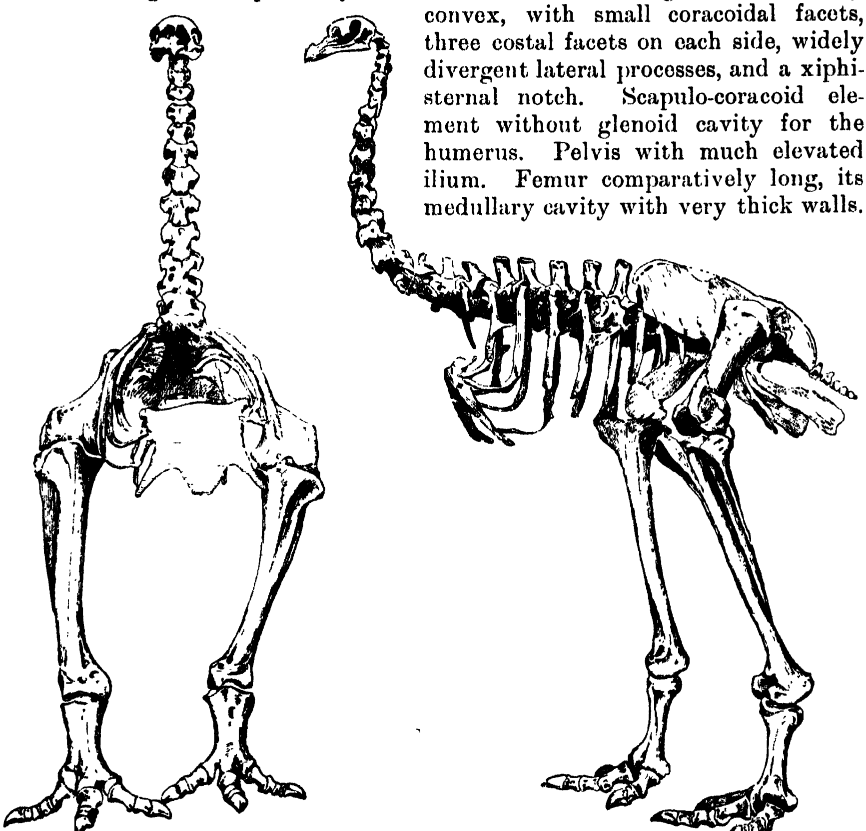


FIG. 529.
Palapteryx elephantopus Owen sp. Pleistocene; New Zealand. $^1/_{18}$ nat. size (after Owen).

Palapteryx Owen (*Emeus* Reichenbach; *Euryapteryx* Haast; *Pachyornis* Lydekker) (Fig. 529). Smaller but much stouter than the preceding. Beak short and rounded; sternum flat, broader than long, without coracoidal facets; pelvis low and broad. Hind limbs extremely massive, tibio-tarsus relatively short; hallux present. Total height less than 2 m.

Anomalopteryx Reichenbach (*Cela*, *Syornis* Reich.; *Mesopteryx* Hutton; *Meionornis* Haast). Small birds of comparatively slender build. Skull narrow and elevated, with sharply-pointed beak. Sternum much longer than

broad, moderately flattened, with faint or no coracoidal facets, three costal facets on each side, and a pair of long and slender lateral processes. Tarso-metatarsus shorter than the femur, and scarcely half as long as the tibio-tarsus; hallux present.

Megalapteryx Haast. Much resembling *Anomalopteryx*, but mandible very slender. Complete skeleton known from cave in S. Island.

Sub-Order 2. APTERYGES.[1]

These are small, flightless birds found only in New Zealand. They are readily distinguished by their long, rather slender beak, and by the nostrils opening at the end of the beak, a unique position among birds. The sternum is broad, the wings are minute, and the foot is four-toed, the first digit being small and above the level of the others. Remains of *Apteryx*, chiefly referable to living species, occur in the superficial deposits of New Zealand.

Sub-Order 3. CRYPTURI.

The tinamous, or *Crypturi*, have a long, narrow keeled sternum, with a long, slender lateral process on either side. In the shortening of the vomer, and moving inwards of the palatines, they show an approach to the *Euornithes*. The tinamous resemble little ostriches in their appearance, and have a limited power of flight. The Sub-Order is specially characteristic of South America, although it extends northwards into Mexico. So far very few fossil remains of the tinamous have been found, and these from comparatively recent deposits. *Tinamisornis* Rovereto seems to be of Pliocene age.

Order 4. EUORNITHES.

Toothless birds. Vomer not in contact with pterygoids, but the latter in contact with the sphenoidal rostrum; quadrate double-headed; mandibular rami fused at symphysis. Ischia fused distally with ilia. Upper half of tarso-metatarsus with canals for passage of tendons. Terminal caudal vertebrae forming a pygostyle.

The *Euornithes* comprise the vast majority of existing birds, and are the equivalent of the *Carinatae*, less *Ichthyornis* and the tinamous. The sternum is generally keeled, although this is a character of little value, since any group may have its flightless forms.

Sub-Order 1. DIATRYMAE.[2]

An extinct group of uncertain affinities. Holorhinal, with desmognathous palate; broad head of quadrate imperfectly divided; squamosal and post-orbital enclosing a supratemporal vacuity. Uncinate processes of ribs reduced. Coracoscapular arch much like that of a Ratite bird; wings greatly reduced. Pelvis wide and long posteriorly; pubes long and almost meeting behind; three-toed foot with a reduced hallux.

Diatryma Cope (? *Barornis* Marsh) (Fig. 530). Skull greatly enlarged,

[1] *Parker, T. J.*, Anatomy and Development of *Apteryx*. Phil. Trans. Roy. Soc., vol. 182 B., p. 25, 1892.

[2] *Andrews, C. W.*, A Gigantic Eocene Bird. Geol. Mag. [6], vol. iv., p. 469, 1917.—*Matthew, W. D.*, and *Granger, W.*, Skeleton of *Diatryma*. Bull. Amer. Mus. Nat. Hist., vol. xxxvii., p. 307, 1917.—*Sinclair, W. J.*, *Omorhamphus*. Proc. Amer. Phil. Soc., vol. lxvii., p. 51, 1928.—*Troxell, E. L.*, *Diatryma*, a Colossal Heron. Amer. Journ. Sci. [5], vol. xxii., p. 18, 1931.

with a powerful laterally-compressed beak and nostril placed low down. Neck short and very powerful. Claws of toes rather short and moderately curved. *D. steini* Matthew and Granger, known by nearly complete skeleton

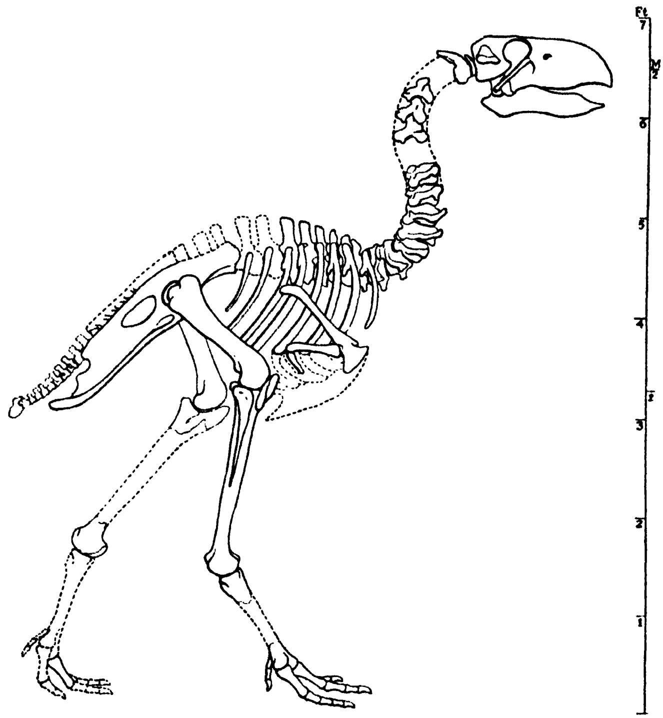


Fig. 530.
Diatryma steini Matthew and Granger. Restoration of skeleton, with scale in feet. Lower Eocene; Wyoming. (After Matthew and Granger.)

2 m. high (Fig. 530) from the Lower Eocene (Wasatch) of Wyoming, U.S.A. Fragments of other species from the same formation in Wyoming and New Mexico, perhaps also New Jersey. ? *D. sarasini* Schaub, a tarso-metatarsus from the Lower Eocene near Epernay.

Omorhamphus Sinclair. Smaller, with a shorter tarso-metatarsus. Lower Eocene; Wyoming.

Sub-Order 2. IMPENNES. Penguins.[1]

In the penguins the wings are shortened, flattened, and modified into paddles, but as they are moved by the muscles employed by other birds in flight, the sternum retains its keel. The skull is schizognathous, and the component bones remain free from one another for an unusual length of

[1] *Ameghino, F.*, Impennes Fósiles de Patagonia y de la Isla Seymour. Anales Mus. Nac. Buenos Aires, vol. xiii., p. 97, 1905.—*Watson, M.*, Report on the Penguins collected by the *Challenger*. Challenger Reports, vol. vii., part xviii., 1883.—*Wiman, C.*, Die alttertiären Vertebraten der Seymourinsel. Wiss. Ergebn. Schwed. Süd-polar Exped., 1901–1903, vol. iii., lief. 1, 1905.—Also *Oliver, W. R. B.*, New Zealand Birds, p. 85, 1930.

time; the pterygoids are very large. The scapula is unique among birds in being expanded posteriorly. The dorsal vertebrae are markedly opisthocoelous. The tarso-metatarsus is short and wide, and its three component metatarsals are plainly indicated by their imperfect fusion.

The penguins are characteristic of the southern parts of the southern hemisphere, but on the west coast of South America they range northwards to the equator. They attained their specialisation at the beginning of the Tertiary period, and remains of several extinct, though typical, genera are known from the Eocene of New Zealand (*Palaeeudyptes* Huxley), the Lower Tertiary (probably Eocene) of Seymour Island, Antarctica (*Anthropornis, Pachypteryx, Eospheniscus, Delphinornis, Ichthyopteryx, Orthopteryx* Wiman), and the Patagonian Formation (probably Miocene) of Patagonia (*Palaeospheniscus* Moreno and Mercerat (Fig. 531), *Paraspheniscus, Perispheniscus, Argyrodyptes* Ameghino, etc.). Some of the extinct species must have been at least 1·3 m. high, and their metatarsus is better adapted for running than that of existing penguins. According to Ameghino, the Patagonian Eocene *Cladornis* Amegh. and *Cruschedula* Amegh. seem to represent terrestrial ancestors of penguins.

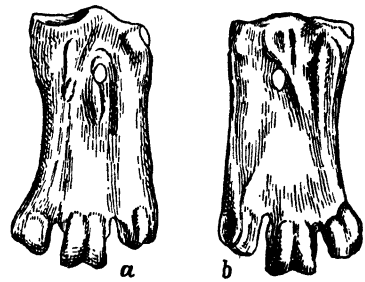


FIG. 531.

Palaeospheniscus planus Ameghino. Left tarso-metatarsus, anterior (*a*) and posterior (*b*) view. Miocene; Patagonia. Nat. size (after Ameghino).

Sub-Order 3. CECOMORPHAE.

The *Cecomorphae* include the auks, gulls, divers, and petrels, these last diverging from the other members of the Sub-Order and often placed in an Order or Sub-Order by themselves, the *Tubinares*. They are all swimming birds, with a schizognathous palate and the angle of the mandible truncate.

The keeled sternum of a gigantic bird apparently of this Sub-Order, from the Eocene of Ameki, S. Nigeria, represents a species twice as large as the largest known albatross, and is named *Gigantornis eaglesomei* Andrews.[1] An albatross, *Diomedea anglica* Lyd., occurs in the Pliocene Red Crag of England, and gulls are numerous in the Miocene of the south of France and Pleistocene of Oregon, U.S.A. *Palaeotringa* Marsh, from the Eocene (not Cretaceous) of New Jersey, seems to be related to the gulls. *Colymboides* Milne Edwards is a diver from the European Eocene and Miocene. *Puffinus* Brisson dates back to the Miocene in both Europe and America. The earliest known auk, *Mancalla californiensis* Lucas, from the Upper Miocene of California, was a highly specialised and flightless form. *Nautilornis* Wetmore, from the Eocene of Utah, seems to have been a wading auk. *Hydrotherikornis* Miller, from the Upper Eocene of Oregon, is probably an allied genus. The Great Auk, *Alca impennis* Linn., a northern bird which became extinct in recent historic times, occurs in Pleistocene deposits so far south as Gibraltar and Otranto, S. Italy.[2]

[1] *Andrews, C. W.*, Sternum of a large Carinate Bird from the Eocene of Southern Nigeria. Proc. Zool. Soc., 1916, p. 519.

[2] *Grieve, S.*, The Great Auk or Garefowl. London, 1885.—*Owen, R.*, Skeleton of the Great Auk. Trans. Zool. Soc., vol. v., p. 317, 1865.

Sub-Order 4. GRALLAE.[1]

The *Grallae* are a group of wading birds including the cranes, bustards, rails, snipe, and plovers, besides an unusual number of aberrant forms, such as the South American trumpeter (*Psophia*), the Seriema (*Cariama*), and the New Caledonian *Rhinochoetus*. The plovers closely approach the gulls among the *Cecomorphae*, while through *Cariama* the *Grallae* point towards the birds of prey.

The *Stereornithes* of Moreno and Mercerat, from the Miocene Santa Cruz Formation of Patagonia, seem to be gralline birds related to *Cariama*. The typical genus *Phororhacos* Ameghino is known by most of the skeleton, and is remarkable for its relatively gigantic head and stout cervical vertebrae. The skull, which measures 60 cm. in length in *P. longissimus* Amegh., has a very large, laterally compressed, hooked beak (Fig. 532), and the nostrils are high up. The furcula is very slender, almost rudimentary, and the wings are small. The pelvis is narrow and elongated. *Pelecyornis* Ameghino and *Brontornis* Moreno and Mercerat are other genera. *Hermosiornis* and *Procariama* Rovereto especially seem to connect the *Stereornithes* with *Cariama*.

Fig. 532.

Phororhacos inflatus Ameghino. Skull and mandible, right side view. Miocene; Patagonia. 1/6 nat. size (after Ameghino).

Graculavus Marsh and *Telmatornis* Marsh, from the Eocene (not Cretaceous) of New Jersey, and *Aletornis* Marsh, from the Eocene of Wyoming, appear to be early representatives of this Sub-Order, and true rails appear in the Eocene of Europe (*Gypsornis* Milne Edwards). A crane (*Palaeogrus* Portis) also occurs in the Upper Eocene of Italy. A coot (*Palaeolimnas* Forbes) is found in surface deposits in the Chatham Islands, about 500 miles east of New Zealand. The extinct rails from the surface deposits of New Zealand (*Aptornis* Owen), the Chatham Islands (*Diaphorapteryx* Forbes; *Nesolimnas* Andrews; *Cabalus* Hutton), and Mauritius (*Aphanapteryx* Milne Edwards) are interesting on account of their close affinities to each other and to the living Weka rail of New Zealand (*Ocydromus* Wagler). The New Zealand rail *Notornis* Owen, now extremely rare, is well known by fossils from the surface deposits of New Zealand. The bustard (*Otis* Linn.) dates back to the Miocene in Europe, and an extinct genus *Palaeotis* Lambrecht occurs in the Middle Eocene Brown Coal of the Geiselthal, Germany.

Sub-Order 5. CHENOMORPHAE.

The *Chenomorphae*, or ducks, form a sharply defined group of water-birds, with the skull typically desmognathous, either by the direct fusion of the maxillo-palatines or their indirect union through the ossified narial septum.

[1] *Andrews, C. W.*, Skull and Skeleton of *Phororhacos inflatus* Ameghino. Trans. Zool. Soc., vol. xv., p. 55, 1899.—Osteology of *Diaphorapteryx hawkinsi*. Novitates Zoologicae, vol. iii., p. 73, 1896; also Geol. Mag., 1896, p. 337.—Osteology of *Palaeolimnas* and *Nesolimnas*. Novit. Zool., vol. iii., p. 260, 1896.—Skeleton of *Aptornis defossor* (Owen). Geol. Mag., 1896, p. 241. —*Sinclair, W. J.*, and *Farr, M. S.*, Aves of the Santa Cruz Beds. Rep. Princeton Univ. Exped. Patagonia, vol. vii., p. 157, 1932.

Low basipterygoid facets are present, well forward on the rostrum; and on these the pterygoids slide, allowing a slight motion of the beak. The posterior end of the mandible is produced and recurved.

Allied to the *Chenomorphae* are three species of South American birds representing the genera *Palamedea* (or *Anhima*) and *Chauna*, which form a separate group, the *Palamedeae*. These birds have neither webbed feet nor duck-like bills.

The flamingoes are assigned by some to the *Chenomorphae*, by others to the *Herodii*, their affinities to both leading Huxley to place them in a separate group termed *Amphimorphae*. *Scaniornis* Dames and *Parascaniornis* Lambrecht, from the Cretaceous of Sweden, may perhaps be ancestral flamingoes.[1] *Agnopterus* Milne Edwards, from the Eocene of the Paris Basin, and *Elornis* Aymard, from the Oligocene and Miocene of France, are also probably flamingoes. Several species of *Palaelodus* Milne Edwards, a shorter-legged bird than the flamingo, also occur in the Miocene of France, and a true *Phoenicopterus* Brisson in the Miocene of France and Pleistocene of Oregon.

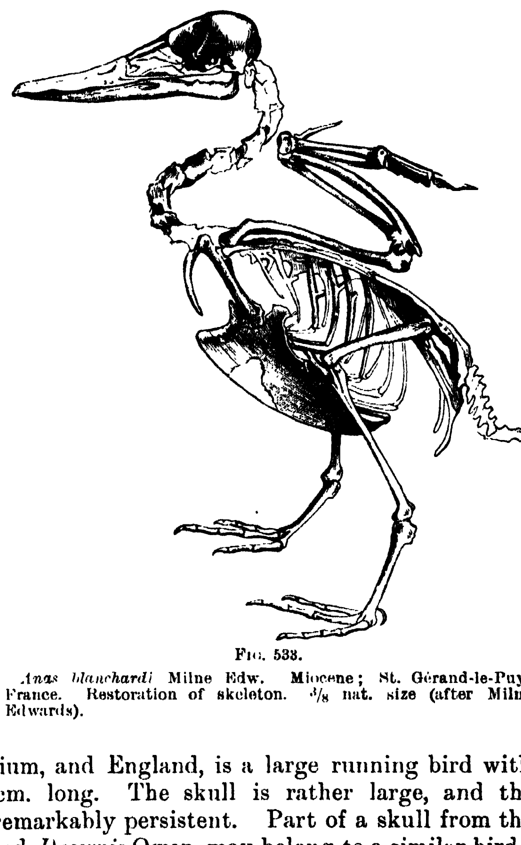


FIG. 533.

Anas blanchardi Milne Edw. Miocene; St. Gérand-le-Puy, France. Restoration of skeleton. $^3/_8$ nat. size (after Milne Edwards).

Gastornis Hébert, from the Lower Eocene of France, Belgium, and England, is a large running bird with a tibio-tarsus sometimes 50 cm. long. The skull is rather large, and the sutures between its bones are remarkably persistent. Part of a skull from the London Clay of Sheppey, named *Dasornis* Owen, may belong to a similar bird.[2]

Ducks are not uncommon in the Miocene of France and Pleistocene of Oregon, and a large, flightless species, *Cnemiornis calcitrans* Owen, occurs in the Pleistocene of New Zealand. This bird well exemplifies the difficulty of determining exact affinities from isolated bones, since from the tibia Owen considered it to be a Moa, while from the sternum Parker believed it to be a rail; the discovery of the skull showed it to be a goose. Numerous species of *Anas* Linn. (Fig. 533), as well as isolated representatives of *Anser*, *Cygnus*,

[1] *Dames, W.*, Vogelreste aus dem Saltholmskalk von Limhamn bei Malmö. Bihang k. svensk. Vet.-Akad. Handl., vol. xvi., sect. iv., no. 1, 1890.—*Lambrecht, K.*, *Gallornis straeleni* n.g. n.sp., ein Kreidevogel aus Frankreich. Bull. Mus. Roy. Hist. Nat. Belg., vol. vii., no. 30, 1931.

[2] *Dollo, L.*, *Gastornis edwardsii*, Lemoine. Bull. Mus. Roy. Hist. Nat. Belg., vol. ii., p. 297, 1883.—*Newton, E. T.*, Remains of *Gastornis klaasseni*, n.sp., from the Lower Eocene near Croydon. Trans. Zool. Soc., vol. xii., p. 143, 1886.—*Owen R.*, Fossil Cranium of *Dasornis londinensis*, Ow., from the London Clay of Sheppey. Trans. Zool. Soc., vol. vii,, p. 145, 1870.

Fuligula, *Spatula*, *Branta*,[1] and *Mergus*, are known from the late Tertiary of various European and North American localities. A femur from the Neocomian of Auxerre, France (*Gallornis straeleni* Lambrecht), may belong to an ancestral goose; *Laornis* Marsh is from the Eocene of New Jersey; and *Romainvillia* Lebedinski, from the Upper Eocene of the Paris Basin, may be related. *Cygnopterus* Lambrecht, from the Upper Oligocene of Belgium, and *Cygnavus* Lambrecht, from the Middle Miocene of Wiesbaden, seem to be ancestral swans.[2]

Sub-Order 6. HERODII.

The *Herodii*, comprising the herons, storks, and ibises, are wading birds with unusually long legs, having a desmognathous skull without basipterygoid processes, and the angle of the mandible usually truncate (exceptions occurring in the spoonbills, *Platalea*).

The herons appear first in the Lower Eocene, *Proherodius* Lydekker occurring in the London Clay of England. *Botauroides* Shufeldt and *Eoceornis* Shufeldt are extinct herons from the Middle Eocene of Wyoming, U.S.A.; and *Goliathia* Lambrecht is represented by a large ulna in the Lower Oligocene of the Fayum, Egypt. Species of the existing *Ardea* Brisson occur in the Middle Miocene of France and Bavaria.

The oldest known stork is *Palaeoephippiorhynchus dietrichi* Lambrecht from the Lower Oligocene of the Fayum, Egypt.[3] *Propelargus* Lydekker and *Pelargopsis* Milne Edwards occur in the Oligocene Phosphorites of France. *Xenorhynchopsis* de Vis and *Palaeopelargus* de Vis are extinct storks from the Pleistocene of Australia. The Indian *Leptoptilus* Lesson occurs fossil in the Pliocene of the Siwalik Hills; *Ciconia* Brisson in the Lower Pliocene of Pikermi, Greece; *Amphipelargus* Lydekker in the Lower Pliocene of the Island of Samos.

An ibis, *Ibidopsis* Lydekker, is found in the Oligocene of England, and *Ibidopodia* Milne Edwards in the Lower Miocene of France. *Protibis* occurs in the Santa Cruz Formation of Patagonia.

Sub-Order 7. STEGANOPODES.[4]

The *Steganopodes* include the pelicans, cormorants, gannets, frigate birds, and tropic birds. They have a desmognathous skull and a sternum with a feeble keel, on the forwardly produced anterior portion of which the lower

[1] *Burt, W. H.*, New Goose (*Branta*) from the Lower Pliocene of Nevada. Univ. Calif. Public., Bull. Dept. Geol. Sci., vol. 18, p. 221, 1929.

[2] *Lambrecht, K*, *Cygnopterus* und *Cygnavus*, zwei fossile Schwäne aus dem Tertiär Europas. Bull. Mus. Roy. Hist. Nat. Belg., vol. vii., no. 31, 1931.

[3] *Lambrecht, K.*, *Palaeoephippiorhynchus dietrichi* n.g., n.sp. *Goliathia andrewsi* n.g., n.sp. Geologica Hungarica, Ser. Palaeont., fasc. 7, pp. 18, 30, 1930.

[4] *Andrews, C. W.*, New Bird from the London Clay of Sheppey [*Prophaethon*]. Proc. Zool. Soc., 1899, p. 776.—Bird Remains from the Upper Cretaceous of Transylvania [*Elopteryx*]. Geol. Mag. [5], vol. x., p. 193, 1913.—*Lambrecht, K.*, Die Gattung *Plotus* im ungarischen Neogen. Mitth. Jahrb. k. ungar. Geol. Reichsanst., vol. xxiv., p. 3, 1916.—Mesozoische und tertiäre Vogelreste aus Siebenbürgen. Xe Congrès Internat. Zool., p. 1262, 1929.—*Pseudodontornis* n.g. Geologica Hungarica, Ser. Palaeont., fasc. 7, p. 1, 1930.—*Protoplotus beauforti* n.g., n.sp. Wet. Meded. Dienst Mijnbouw Nederl.-Indie, no. 17, p. 15, 1931.—*Owen, R.*, *Odontopteryx toliapicus* Ow. Quart. Journ. Geol. Soc., vol. xxix., p. 511, 1873.—*Argillornis longipennis* Ow. *Loc. cit.*, vol. xxxiv., p. 124, 1878, and vol. xxxvi., p. 23, 1880.—*Wetmore, A.*, Systematic position of the fossil bird *Cyphornis magnus*. Canadian Geol. Surv. Bull. no. 49 (Geol. Ser., no. 48), 1928.

ends of the clavicles rest and are frequently joined by anchylosis. A distinctive external feature is the union of all four toes by a web.

Pelecanus Linn. occurs in the Miocene of Bavaria and Allier, France, and is also found in the Pliocene of the Siwalik Hills, India. The existing *P. onocrotalus* Linn. is found in the deposits of the English Fenland, in a similar deposit at Hull, and with the remains of the Iron Age in the Glastonbury Lake Village; another species in the Pleistocene of Oregon, U.S.A. Cormorants date back at least to the Lower Eocene. *Argillornis* Owen is known by a skull and other bones from the London Clay of Sheppey; *Eupterornis* Lemoine by a portion of ulna from the Lower Eocene, Rheims, France. *Actiornis* Lydekker is from the Oligocene of Hordwell, Hampshire. *Elopteryx* Andrews, represented by bones of hind limb from the Upper Cretaceous (Danian) of Transylvania, may be an ancestral cormorant. *Eostega* Lambrecht, from the Middle Eocene of Transylvania, is also related. *Odontopteryx* Owen, from the London Clay of Sheppey, belongs to an allied family with bony denticles along the edge of the jaws. A more generalised desmognathous skull, with similarly denticulated jaws, is known from an unrecorded formation and locality in Brazil (*Pseudodontornis* Lambrecht). It must have been about 40 cm. long. *Sula* Brisson dates back to the Oligocene in Europe, the Miocene in North America. *Cyphornis* Cope, from the Oligocene of British Columbia, and *Palaeochenoides* Shufeldt, from the Miocene of South Carolina, are related. *Prophaethon* Andrews is a primitive tropic bird known by the skull and other parts of the skeleton from the London Clay of Sheppey. In this fossil the pelvis and hind limbs are relatively larger than in the existing *Phaethon*. The darter *Plotus* ranges from the Lower Pliocene upwards in Europe, and *Protoplotus* Lambrecht occurs in the Middle Tertiary of Padang, Sumatra.

Sub-Order 8. OPISTHOCOMI.

The *Opisthocomi* contain only a single species, the hoactzin (*Opisthocomus cristatus*) of tropical South America. In the nestling the thumb is large, clawed, and used with the second clawed digit in climbing; but in the adult it is clawless, and even smaller than in the majority of birds, being a remarkable instance of rapid retrogression. *Filholornis* Milne Edwards, from the Oligocene Phosphorites of Southern France, has been referred to this Sub-Order, but its position is doubtful.

Sub-Order 9. GALLINAE.

The earliest known Gallinaceous bird is a primitive pheasant, *Palaeophasianus* Shufeldt, in the Lower and Middle Eocene of Wyoming. *Phasianus* Brisson is itself recorded from the Middle Eocene of Wyoming, and ranges to the Miocene in Nebraska. Though no longer native in Europe, *Phasianus* is also found in the Miocene and Pliocene of this continent, and it occurs in the late Pleistocene of France and Spain.[1] *Gallinuloides* Eastman is a generalised form known by a skeleton from the Middle Eocene of Wyoming.[2] *Taoperdix*

[1] *Gaillard, C.*, L'Origine du faisan d'Europe. Compte rendu Assoc. Franç. Avanc. Sci., Lyon, p. 408, 1926.

[2] *Eastman, C. R.*, New Fossil Bird from the Middle Eocene of Wyoming. Geol. Mag. [4], vol. vii., p. 54, 1900.

Milne Edwards is from the Upper Eocene, *Palaeoperdix* M. Edw. from the Middle Miocene of France.[1] *Palaeortyx* M. Edw. and *Paraortyx* Gaillard are partridge-like birds from the Upper Eocene to Middle Miocene of France. *Palaeocryptonyx* Depéret is Oligocene and Pliocene. *Gallus* Brisson is first found in the Lower Pliocene of Pikermi, Greece. *Thiornis* Navás is found in the Oligocene of Teruel, Spain. *Parapavo* L. H. Miller is a turkey from the Pleistocene asphalt deposit of Rancho la Brea, California.[2]

Sub-Order 10. COLUMBAE.

The pigeon *Columba* Linn. is first found in the Miocene of Allier, France, and *Pterocles* Temminck occurs both here and in the Phosphorites of Quercy. The most important extinct members of the Sub-Order are the dodo (*Didus ineptus* Linn.) from Mauritius and the solitaire (*Pezophaps solitaria* Gmelin sp.) from Rodriguez, both found in modern superficial deposits.[3] They were heavy ground pigeons, and were probably exterminated in the seventeenth and eighteenth centuries respectively.

Sub-Order 11. ACCIPITRES.

The *Accipitres* include the diurnal birds of prey, the American vultures, and the secretary bird. They have an imperfectly desmognathous skull, the spongy maxillo-palatines being only partly united with one another, and in some species even free. Basipterygoid facets are absent in the diurnal birds of prey, but present in the other members of the Sub-Order.

The oldest known fragment of an accipitrine bird appears to be a sternum associated with other fragments from the London Clay of Sheppey (*Lithornis vulturinus* Owen). *Palaeocircus* Milne Edwards occurs in the Upper Eocene of France and the Lower Oligocene of Hordwell, England. *Phasmagyps* Wetmore and *Palaeogyps* Wetmore in the Oligocene of Colorado. *Aquila* Brisson dates back to the Middle Eocene in Wyoming, to the Lower Miocene in Allier, France. *Milvus* Lacépède and an extinct genus *Palaeohierax* Milne Edwards also occur in Allier. A vulture (*Palaeoborus* Coues) is found in the Upper Miocene of New Mexico. *Teratornis* L. H. Miller is a condor-like vulture, larger than the existing condor, found with other accipitrine birds in the Pleistocene asphalt of Rancho La Brea, California,[4] also in the Pleistocene of Florida. *Harpagornis* Haast is a very large extinct eagle from Glenmark Swamp, Canterbury, New Zealand. A primitive secretary bird, *Amphiserpentarius* Gaillard, occurs in the Oligocene Phosphorites of Quercy, and *Serpentarius* Cuv. itself is recorded from the Lower Miocene of Allier.

[1] *Eastman, C. R.*, Fossil Avian Remains from Armissan. Mem. Carnegie Mus., vol. ii., p. 131, 1905.

[2] *Howard, H.*, A Review of the Fossil Bird *Parapavo californicus* (Miller). Bull. Dept. Geol. Univ. California, vol. xvii., no. 1, 1927.—*Sushkin, P. P.*, Affinities of *Parapavo californicus* (Loye Miller). Ibis, Jan. 1928, p. 135.

[3] *Günther, A.*, and *Newton, E.*, Extinct Birds of Rodriguez. Phil. Trans. Roy. Soc., vol. 168, p. 423, 1879.—*Melville, A. G.*, and *Strickland, H. E.*, The Dodo and its Kindred. London, 1848. —*Newton, A.* and *E.*, Osteology of the Solitaire. Phil. Trans. Roy. Soc., vol. 159, p. 327, 1869. —*Newton, E.*, and *Clark, J. W.*, Osteology of the Solitaire. *Loc. cit.*, vol. 168, p. 438, 1879.—*Oudemans, A. C.*, Dodo Studien. Verhandl. k. Akad. Wet. Amsterdam, sect. 2, vol. xix., no. 4, 1917.—*Owen, R.*, Memoir on the Dodo. London, 1866.—Osteology of the Dodo. Trans. Zool. Soc., vol. vi., p. 49, 1867.

[4] *Stock, C.*, Rancho La Brea. Los Angeles Museum, publ. no. 1, 1930.

Sub-Order 12. PSITTACI.

The *Psittaci*, or parrots, have a desmognathous skull without basipterygoid facets, and the beak is so hinged to the cranium as to permit considerable movement.

Fossil parrots are rare, but the African genus *Psittacus* Linn. is found in the Miocene of Allier, France. *Conuropsis* Salvadori occurs in the Middle Miocene of Nebraska.

Sub-Order 13. STRIGES.

In all the owls the orbits face forwards, and the outer toe is reversed. *Minerva* Shufeldt, from the Middle Eocene of Wyoming, is the earliest genus known. *Necrobyas* Milne Edwards and *Strigogyps* Gaillard are extinct genera in the Phosphorites of Quercy, France, in which *Bubo* Cuvier and *Asio* Brisson are also recorded. *Strix* Linn. ranges upwards from the Lower Miocene in Europe.

Sub-Order 14. PICARIAE.

This is not a natural assemblage, and no diagnosis based on osteological characters alone can be framed to include all members, though a better agreement is to be found in the pterylosis and muscles. The hypotarsus never contains the number of tendinal perforations found in the *Passeres*, and there are often peculiarities in the arrangement of the toes; thus some swifts and goatsuckers have the number of phalanges 2, 3, 3, 3; the woodpeckers, cuckoos, and toucans have the fourth toe reversed; in the colies the first toe may be turned forwards; and in the trogons the first and second toes are directed backwards. The *Pici*, characterised by a degenerate palatal structure, and the decurved end of the scapula, are united by Fürbringer with the *Passeres* to form his *Pico-Passeres*.

The hinder part of a skull from the London Clay of Sheppey (*Halcyornis* Owen) has been compared with that of a kingfisher, but its affinities are doubtful.

Uintornis Marsh, related to the woodpeckers, and *Cryptornis* Gervais, a relative of the hornbills, occur in the Eocene of Wyoming and France respectively. *Cypselus*, *Limnatornis*, a hoopoe, *Trogon*, and *Necrornis*, one of the *Muscophagidae*, are from the Oligocene and Miocene of France, the last two hinting at a former more northerly extension of the African avifauna. *Archaeotrogon* Milne Edwards, *Geranopterus* M. Edw., and *Cypselavus* Gaillard are extinct genera in the Quercy Phosphorites.

Sub-Order 15. PASSERES.

The Sub-Order *Passeres* embraces about one-half of the existing species of birds, mostly of small size, the raven being the giant of the Sub-Order, widely distributed over the globe. The skull is aegithognathous.[1]

Except in *Cholornis*, in which the fourth toe is a mere vestige, there are three toes in front and one behind; the hypotarsus is more highly specialised

[1] *Parker*, *W. K.*, On the Skull of Aegithognathous Birds. Trans. Zool. Soc., vol. ix., p. 289, 1873; vol. x., p. 251, 1878.

than in any other group, having four large tendinal perforations, and sometimes two smaller ones in addition.

The earliest *Passeres* occur in the Middle Eocene of Wyoming (*Hebe* Shufeldt), and in the Upper Eocene of the Paris Basin (*Palaegithalus* Gervais and *Laurillardia* Milne Edwards). *Palaeospiza* Allen is found in the Miocene of Colorado. These and all later remains are very fragmentary.

In conclusion, it may be well to repeat that our knowledge of the phylogeny of the various groups of birds is very imperfect, and that most of the fossil forms are not only representatives of well-known families, but often belong to the same genera as species now living in the same geographic area in which the fossils occur. This is in marked contrast with what we find in the Mammalia, for not a family of these occurring in the Eocene, and few in the Miocene, are represented by living species.

From the fact that the majority of birds possess the power of flight they throw little light on the problems of former land connections and lines of distribution, although they may to some extent indicate climatic differences between the past and the present. There is a great gap between the birds of the Eocene and the toothed birds of the Cretaceous, and a greater one between these and the Jurassic *Archaeopteryx*, while the point at which birds diverged from reptiles and assumed feathers is still unknown.

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